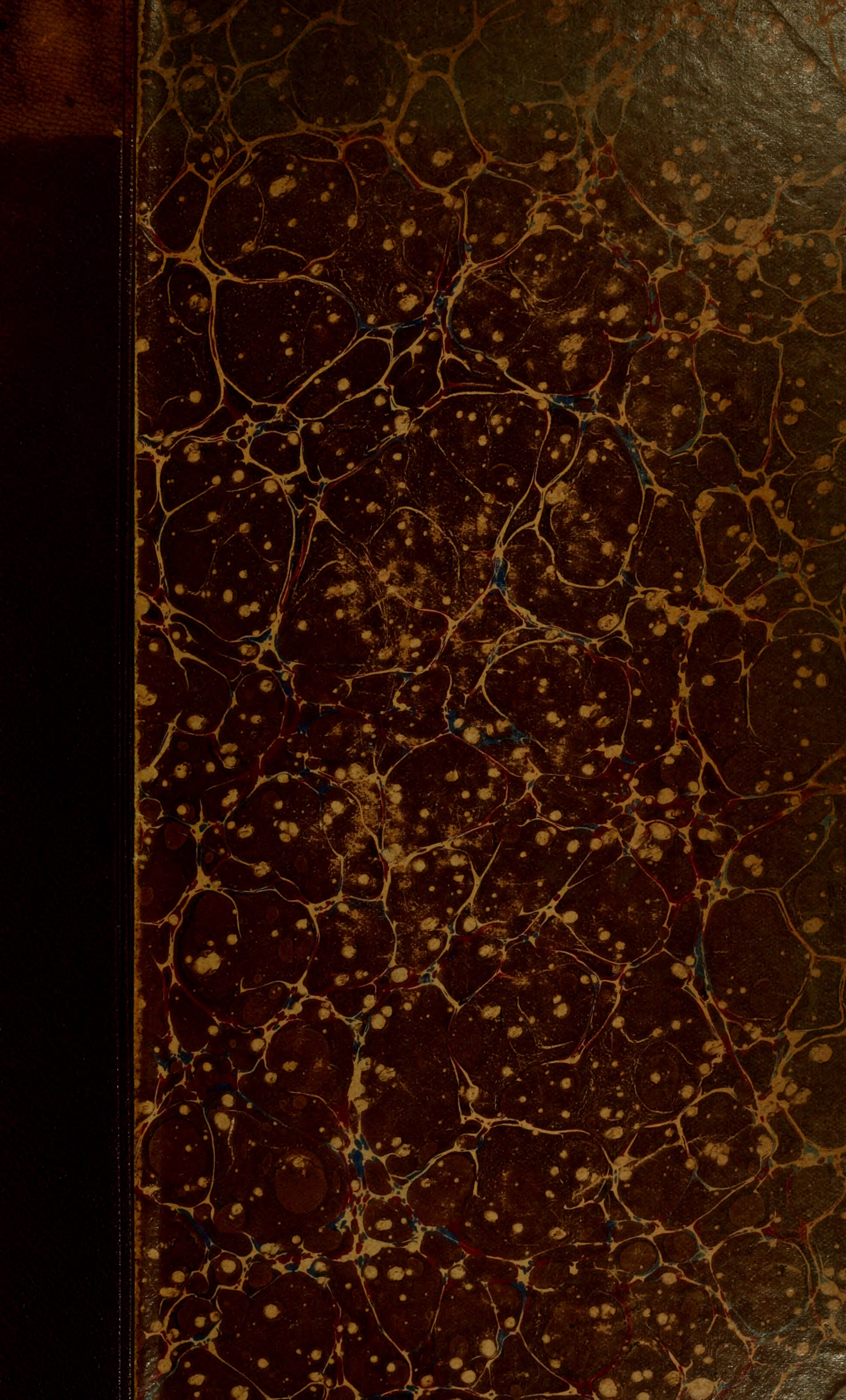

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NEW YORK BOTANICAL GARDEN
VOL. II.

THE INFLUENCE OF LIGHT AND DARKNESS UPON GROWTH AND DEVELOPMENT

BY
DANIEL TREMBLY MACDOUGAL, PH.D.

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PREFACE.

The results described in the following pages were obtained by a series of experimental observations begun in 1895 and continued until the close of the year 1902. Originally designed to analyze the phenomena of etiolation, the work has naturally led to a consideration of the more general relations of the plant to light, and it is believed that some important additions to the knowledge of the subject have been made. The chief results of value have been obtained by long continued confinement of the etiolating plants in dark chambers from which light was entirely excluded.

The author has received material assistance from his students and colleagues during the seven years over which the investigations extended. The description of the etiolation of *Oxalis* and *Sarracenia purpurea* is largely drawn from examinations of etiolated specimens made by Mr. Wm. B. Stewart. A number of botanists have rendered notable aid in the interpretation of some of the morphological facts presented.

The illustrations are from drawings made from the actual objects or photographs, by Miss Alexandrina Taylor and Mr. August Mariolle.

D. T. MacDougal.

New York Botanical Garden, Jan. 10, 1903.

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THE INFLUENCE OF LIGHT AND DARKNESS UPON GROWTH AND DEVELOPMENT.

HISTORICAL.

The more apparent features of the behavior of plants in darkness must have been a matter well known to cultivators from the earliest times, but a conception of the influence of light upon growth and form seems to be a distinctly modern idea. John Ray appears to be the first botanist to make mention of the more apparent features of etiolation, and of the relation of color to illumination.[1]

The quantitative effects of illumination of various degrees of intensity was known to Hales in a way, and he saw that diffuse light did not permit or induce normal development as he says: "Beans and many other plants, which stand where they are much shaded, being thereby kept continually moist, do grow to unusual heights, and are drawn up as they call it, by the overshadowing trees, their parts being kept long, soft and ductile." Hales also made the observation that plants become heavier at night.[2] So far as may be learned from the records consulted, Bonnet may be designated as the pioneer in actual experimental investigation of the subject. He carried out a series of tests upon beans, peas, and branches of the vine, from which it was seen that elongated internodes and small yellow leaves were produced in darkness. Etiolated plants became green after exposure to illumination for 24 hours. Green leaves placed in darkness did not blanch, but fell from the stems. The wood of etiolated stems did not "harden" and cuttings from etiolated stems could not propagate the plant.[3]

After Bonnet, Mees may be named as having carried out the next important experimental observations, which covered a large number of the phases of the question still under discussion. Mees saw that some seeds germinate in darkness as well as in light, that red color

[1] Ray, J. Historia Plantarum, 1: 15. 1686. Also in imprint of 1693.

[2] Hales, S. Statical Essays, 1: 334. 1727. Also p. 336. Ed. of 1769.

[3] Bonnet, Ch. Usage des feuilles, p. 254. 1754.

is formed as usual in etiolated leaves, that aquatic plants may be etiolated, that perfect seed formation does not occur in darkness except in subterranean plants, that flowers which open in darkness perish more quickly than similar ones in light, that growth is more rapid during the first stages of etiolation, and that etiolated plants take up and transpire less water than the normal.[4] It is remarkable that these earlier observations agree almost point by point with those which will be described in the concluding section of this memoir.

Duhamel recounted the observations of Bonnet in 1758, but it can not be learned that he made any independent experimental investigation of the subject.[5]

Knowledge of etiolation was notably increased as a result of Senebier's observations, which were first published in 1782. Senebier found that etiolated stems of the bean were greater in diameter and developed more hairs than the normal plant. The epidermal cells were seen to be more irregular in outline than those of etiolated plants, and were separated from the underlying tissues by smaller intercellular spaces, and the pith was greater in amounts in etiolated plants. The emergence of the flowers of certain monocotyledonous plants in normal and etiolated specimens was thought to be dependent upon qualities of the sheath induced by etiolation or illumination. Peduncles were seen to undergo excessive elongation in darkness and some changes in colors were observed. Mosses were seen to blanch when placed in darkness for long periods.[6]

Twenty-eight years later Senebier gave a comprehensive summary of the subject, in which he noted minor observations by Linnaeus, Humboldt, and others. He made the first estimations from which it was seen that the dry weight of etiolated plants is less than the normal, and formulated a hypothesis to account for the phenomena of etiolation, which asserted that the basal or primitive color of plants was yellow, and that coloration was due to the fixation of carbon and elaboration of the carbon compounds. The absence of illumination prevented the assimilation of carbon dioxide and the construction of coloring and other matter.[7]

---

[4] Mees' observations were published after his death by Van Swinden in the Journal de Physique, **6**: 445. 1776, and **7**: 112, 193.

[5] Duhamel du Monceau. Des plantes étiolées, in La physique des arbres, **2**: 155. 1758.

[6] Senebier, J. Mémoires physico-chimiques, **2**: 51–116. 1782.

[7] Senebier, J. Physiologie végétale, **4**: 264–308. 1800.

A number of scientists made observations of various kinds upon the relations of light to plants in the closing period of the eighteenth century, which resulted in the discovery of the simple elements, and the foundation of chemistry. Attention was chiefly directed to the evolution and absorption of gases in darkness and in light, but incicentally some information was acquired as to changes in form as induced by various degrees of illumination, or by darkness. Tessier[8] tested the formation of green color in red yellow, and white light and of illuminations from lamps and the moon. Some striking effects in phototropism were obtained. Senebier exposed plants to isolated portions of the spectrum, and to illuminations of various intensities, finding that growth was more rapid in violet rays than in red, and that white light was more active than any of its constituents. De Saussure[9] concluded as a result of his own work and the results of others that light was without effect upon growth as manifested by germinating seeds.

DeCandolle[10] describes some work done by him upon etiolation in 1799, in which he notes the blanched appearance of the undeveloped leaves formed by etiolated seedlings of *Sinapis album*, *Lepidium sativum*, and *Miagrum sativum*, together with the phenomena attendant on the excessive elongation of stems, which ensued in darkness. Several years later he gave the matter somewhat more comprehensive treatment in his text-book on plant physiology. In the latter essay he sets forth that sunlight increases the suction of roots and causes transpiration. Cessation of illumination, as in etiolation, stops transpiration, while absorption continues and the plant becomes highly charged with water or "hydropique." The formation of coloring matter in flowers in the darkness was observed. Non-green organs were supposed to be but little affected by etiolation. He also made partial etiolations by thrusting the tips of branches into dark chambers, although he was not the first to try this experiment as asserted by G. Kraus, Bonnet having made similar tests a half century before.

Link[11] reported that etiolated shoots were pale in the earlier stages but became green later, no doubt due to defective methods of exclusion of light.

---

[8] Tessier. Expériences propres à dévelloper les effets de la lumière sur certaines plantes. Mém. l'Acad. d. Sc. Paris, p. 133. 1783.

[9] De Saussure, Th. De l'influence de la lumière sur la germination. Recherches chimiques sur la végétation, p. 21. 1804.

[10] DeCandolle, A. P. Expériences relatives à l'influence de la lumière sur quelques végétaux. Mem. Math. et phys. Inst. Nat. Paris, 1 : 332. 1806. (Presented in 1799.)

[11] Link, D. H. F. Grundlehren der Anat. u. Physiol. d. Pflanzen. p. 291. 1807.

J. E. Smith[12] records that when light was admitted to leaves through glasses of different colors, the plants became paler as the glass approached violet in tint. He reiterates the mistaken idea that blanched plants become green when exposed to the action of hydrogen. From a consideration of currently accepted descriptions he concludes that light acts beneficially on the upper surfaces of leaves, and hurtfully on the lower sides, hence the upper is always turned toward the illumination.

DeCandolle[13] also exposed a number of plants to the light from six argand burners, which was insufficient to cause the release of oxygen, yet it was found that this illumination would cause the formation of chlorophyl in etiolated specimens.

Rè[14] used the term "clorosi" to denote the blanching of plants when deprived of light, as distinct from the modern usage, and related that many "salads" were treated to induce this condition ("asparagi, sedani, e cardi").

Knight[15] was cognizant of the effects of deprivation of illumination, and he developed a new method of culture of rhubarb in darkness and diffuse light in order to increase its succulence and edibility. His experimental results upon the influence of light upon the formation of the tubers of the potato have also become of great importance in experimental morphology and physiology.

Sir Humphrey Davy[16] made analyses of normal and etiolated material in which he found that 400 grains of leaves grown in sunlight yielded 53 grains of woody fiber after being subjected to the action of boiling water and alcohol, and that an equal amount of etiolated material gave but 31 grains of "woody fiber." Poggioli[17] found that plants developed better in violet rays than in red, probably referring to the greater elongation of the stems which ensues under such circumstances.

---

[12] Smith, J. E. An Introduction to Systematic and Physiological Botany. Pp. 206, 207. 1807.

[13] DeCandolle, A. P. Physiologie végétale, 3: 1069. 1832.

[14] Rè, F. Saggio di nosologia vegetabile. P. 23. 1807.

Rè, F. Saggio Teorico-Pratico sulle Malat ie delle piante. P. 147. 1807.

[15] Knight, T. A. On a method of forcing rhubarb in pots. Trans. Hort. Soc. Lond. 3: 154. 1820. See also a selection from the physiological and horticultural papers published in the Transactions of the Royal and Horticultural Societies. 1841.

[16] Davy, H. Elements of Agricultural Chemistry. Pp. 208, 209. 1815.

[17] Poggioli, S. Opuscules scientifiques de Bologne, 1: 9.

Fries[18] as early as 1821 recognized the influence of light upon fungi and saw that many forms including the Hymenomycetes, and the Pezizaceae remain sterile and do not form spores when deprived of illumination, and that many variations in form, notably excessive elongation and branching, resulted from such treatment. Montagne[19] saw that light did not exert the same influence upon the mycelium and sporophore, and Bonorden believed that the coloration of agarics and other fungi was dependent upon light. In this last conclusion however other mycologists were not agreed. The necessity of illumination to induce the formation of spores was also recognized by Tulasne.[20]

The period from 1820 to 1842 is devoid of literature upon the relations of light to the higher plants in so far as the aspect of the subject in question is concerned. The text-books appearing about the latter date and preceding the wonderful renascence of botany under the influence of Sachs appear to ignore the observations of the mycologists and to assume that light could have an effect only upon green plants.[21]

Beginning with the work of Payer[22] in 1842, several distinct series of investigations upon the relations of green plants to light may be distinguished. One dealt with the analysis of the values of the different portions of the spectrum in the formation of food, the production of curvatures and general influence upon growth. A second was devoted chiefly to the formation and activity of chlorophyl, the nature of chlorophyllary, synthetic and decomposition products. The third, which was first taken up seriously by Sachs, was concerned with the morphogenic influence of light and with all of the multifarious phenomena of etiolation. It will be unnecessary in the present connection to inquire into literature which does not bear directly upon the results of etiolations and the influence of light upon growth. Neither will attention be given to papers dealing with the more strictly morphological aspects of the influence of light upon form, as in dorsiventrality, etc.

---

[18] Fries, E. Systema mycologicum, **1**: 502. 1821. Also **3**: 265. 1839. And Syst. Orb. Veg. **1**: 212. 1825.

[19] Montagne. Esquisse organographique et physiologique sur la classe champignons. 1841.

[20] Tulasne. Fungi hypogaei. P. 2. 1852.

[21] Lèveillè. Considerations mycologiques. 1846.

Bonorden. Handbuch der allgemeine Mykologie. 1851.

Schmitz, J. Beiträge zur Anatomie und Physiologie der Schwämme. Linnaea, **17**: 475. 1843.

De Bary. Recherches sur le développement de quelques champignons parasites. Ann. Sc. Nat. IV. **20**: 40, 54. 1863.

[22] Payer. Mèm. sur la tendance des racines à fuir la lumière. Compt. rend. d. l. Acad. d. Sc. **1**: 1194. 1842.

Payer, Gardner[23] and Draper[24] investigated the activity of chlorophyl in various parts of the spectrum and also the general facts now included under phototropism. Draper made cultures of peas in blue light and in darkness. He notes that seedlings under the latter condition are pale yellow with no fresh leaves, and that a height of thirteen times the normal was attained with the etiolated plant apparently into a vigorous condition. Dutrochet[25] confirmed Payer's results in the main.

Meanwhile but little of the information gained by the late investigations found its way into the text-books of botany. Carpenter[26] gave the substance of DeCandolle's conclusions in 1848, and saw in the non-development of woody fiber and of secretions the most important results of etiolation. The blanching of celery, sea kale and other plants was recorded, and it may be assumed that this treatment of salad plants was in more or less common practice at that time. He cites the following diverting illustration of natural etiolations, which is to be found in many European text-books of the period: "It frequently happens in America that rain and clouds obscure the atmosphere for several days together; and that during that time the buds of entire forests expand themselves into leaves. These leaves assume a pallid hue until the sun appears; when within the short period of six hours of a clear sky and a bright sunshine their color is changed to a beautiful green." Another writer fortifies this statement with the additional fancy "that a forest in which the sun has not shone for twenty days, the leaves were expanded but were almost white. One forenoon the sun began to shine in full brightness: the color of the forest changed so fast that we could perceive its progress."

An analysis of etiolated specimens of *Pisum sativum*, *Hordeum vulgare* and *Avena sativum* by Vogel[27] in 1856 led him to the generalization that etiolated plants contained 2 per cent. more water than normal specimens. The ash constituent showed an increase of 4 per cent. and the proportion of carbon decreased. Measurements of root systems suggested a more marked development of these organs than those of plants in light.

---

[23] Gardner. London, Edinburgh and Dublin Philosophical Magazine. 1844.

[24] Draper. Chemistry of plants. 1844. New York.

[25] Dutrochet. Rapport sur un mémoire de M. Payer intitulé: Mémoire sur la tendance des racines à fuir la lumière. Ann. Sc. Nat. III. **2**: 96. 1844.

[26] Carpenter, M. B. Vegetable Physiology, and Systematic Botany. P. 198. 1848.

[27] Vogel, A. Beiträge zur Kenntniss der Verhältnisses zwischen Licht und Vegetation. Flora, **39**: 385. 1856.

Guillemin[28] states that etiolated plants developed green color more rapidly in blue, yellow, green, and orange or red, than in direct sunlight, and that the action of yellow light was equal to that of diffuse daylight.

The chemical nature of chlorophyl and the manner of its formation engaged the attention of a number of authors. Gris[29] made a series of investigations upon the behavior of chloroplasts and the formation of chlorophyl in 1857 in which he etiolated plants of *Sempervivum tectorum*, *S. Haworthii*, *Sedum dendroideum*, *Aloe obliqua*, *Vicia Faba*, *Oxalis*, bean and erythrine. Chloroplasts appeared to diminish in size during the process of blanching. Some data were given by him concerning the form and character of the protoplasm of etiolated organs to which reference will be made in a later part of this paper.

Sachs[30] began the study of etiolation phenomena and the publication of his results in 1859, and interest in this subject was most active in the decade following, numbers of investigations being carried on in the Würzburger laboratory by Sachs and his students, and by other workers in Germany, France and England.

Sachs'[31] earliest observations were concerned with the relations of light to chlorophyl principally, as well as the origin of starch, but as may be seen a widening attention was given the subject, and growth, development, and stature of etiolated plants were dealt with in great detail. Sachs saw the construction of chlorophyl in cells in which he thought the chloroplasts had not yet assumed form, and the degeneration of these bodies was seen in etiolated examples of *Cucurbita*, *Zea Mais*, and *Helianthus annuus*. He noted that germinating bulbs of *Allium Cepa* produced leaves of the usual length in darkness, but these organs were more slender and thinner, not showing the central lysigenetic cavity. The protoplasm in this plant as well as in *Beta vulgaris*, *Apium graveòlens*, *Zea*, *Helianthus*, *Phaseolus*, and *Cucurbita* grown in darkness appeared highly granular.

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[28] Guillemin, C. M. Production de la chlorophylle, et direction des tiges sous l'influence des rayons ultra-violets, calorifiques. et lumineux du spectre solaire. Ann. Sc. Nat. IV. 7: 154. 1857.

[29] Gris, A. De étiolement. Recherches microscopiques sur la chlorophylle. Ann. Nat. Sci. IV. 7: 207. 1857.

[30] Sachs. Handbuch d. physiol. Bot. 1865. See Lotos, Jan. 1859.

[31] Sachs. Ueber den Einfluss des Lichtes auf die Bildung des Amylums in den Chlorophyllkörnern. Bot. Zeitung, 20: 365. 1862.

Sachs. Uebersicht der Ergebnisse der neueren Untersuchungen ueber das Chlorophyll. Flora, 45: 129. 1862.

Sachs. Ueber den Einfluss des Tageslichtes auf Neubildung und Entfaltung verschiedener Pflanzenorgane. Bot. Zeitung, 21: Beil. 31. 1863.

Seedlings grown in darkness appeared to continue existence until all of the reserve material in the seed was exhausted, and then died unless brought into light of an intensity sufficient to cause the formation of food at such rates as to show the presence of starch in the leaves. Starch was always found in the guard cells of the stomata of such presumably starved specimens. It is well established by the results of more recent workers that the seedling rarely if ever totally exhausts the available supply of food in the seed.

Normal stomata were produced by etiolated plants of *Beta vulgaris*, *Dahlia variabilis* and *Phaseolus multiflorus*, except that the chloroplasts were in the etiolated condition.

Inflorescences of *Nicotiana* thrust into a dark chamber unfolded the corollas normally and produced seeds of a size above the normal, which germinated in the usual manner. Adventitious roots were formed in great abundance on portions of stems of *Phaseolus*, *Vicia Faba*, *Helianthus tuberosus*, *Cactus speciosus* and *Cicuta virosa* in darkness much more abundantly than in light; many of these plants not forming such organs in light. A group of monocotyledonous species included in *Zea*, *Triticum*, *Crocus*, *Iris*, *Hyacinthus*, *Tulipa* and *Allium* formed etiolated leaves of a length greatly in excess of the normal, but of inferior width in darkness.

Hyacinthus leaves attained an exaggerated length but the laminae were rolled up in cylindrical form, an observation which was confirmed by my own observations. Leaves of *Tragopogon porrifolius* were of the customary length in darkness, while those of *Phaseolus*, *Tropaeolum*, *Humulus*, *Begonia* and *Solanum* attained only a fraction of their normal size in darkness, and in some species retained the position assumed in the bud. Etiolated specimens of *Bryonia* bore tendrils of average size which were normally sensitive and were able to grasp supports; an observation previously made by von Mohl. Leaves of

Beta vulgaris attained greater length in light than in darkness. Cotyledons of *Mirabilis Jalapa*, *Brassica*, *Polygonum*, *Fagopyrum*, *Cucurbita* and *Helianthus* did not attain normal size. Fronds of *Pteris chrysocarpa* grown in darkness were green in color in accordance with results previously attained by DeCandolle. Hypocotyls of *Fagopyrum*, *Cucurbita Pepo*, *Brassica*, *Napus*, *Phaseolus multiflorus* and *Tropaeolum majus* were excessively elongated in darkness, reaching twenty times the normal length. Scapes of *Hyacinthus orientalis*, *Tulipa Gesneriana* and *Iris pumila* were greatly elongated in darkness, while the scape of *Crocus verna* remained of average length but showed an excessive growth of the perianth tube.

Internodes of *Dioscorea Batatas* and *Bryonia dioica* did not increase beyond the average normal length, although such increase was observed in *Phaseolus multiflorus*. The short thick stems of beets and cacti did not elongate beyond the normal in darkness, and the diameter of etiolated stems of *Phaseolus multiflorus*, *Vicia Faba*, *Dioscorea Batatas* and *Tropaeolum* showed but little variation from the ordinary measurements. The hypocotyl of *Cucurbita Pepo*, which is cylindrical in cross section in normal plants, was more or less flattened in etiolated examples.

Normal torsions were found in etiolated stems of *Bryonia* and other climbers, and are also exhibited by many species in which such properties are not usually present, such as the hypocotyl of *Mirabilis Jalapa*, *Brassica Napus*, *B. oleracea*, *Cheiranthus Cheirii*, *Linum grandiflorum*, *Helianthus annuus*, scapes of *Hyacinthus orientalis*, internodes of *Vicia Faba*, cotyledons of *Scorzonera Hispanica*, and leaves of *Hyacinthus orientalis*. A great diversity of reaction was exhibited by flowers. According to Sachs' results flowers of *Tulipa*, *Hyacinthus*, *Iris* and *Crocus* reach an advanced stage of development in darkness, although the facts adduced are not confirmed by my own observations. Flowers of *Brassica*, *Tropaeolum*, *Papaver*, *Cucurbita* and others might not carry on their entire development in darkness, but if the buds were allowed to reach the stage immediately preliminary to opening or thereabouts, in light, flowers of reduced size, but normal structure, were produced.

Sachs' investigations upon this subject were continued for about fifteen years, and received some attention during the remainder of his lifetime. In addition to the papers cited other brief notes were published and the entire subject was discussed in his collected works.

Among the additional facts obtained it is to be noted that *Veronica speciosa* developed normal flowers and fruits and also *Ipomoea purpurea*. A fruit of *Cucurbita Pepo* weighing 472.5 grams was produced in darkness. Seeds of this fruit, as well as those of *Allium porrium* and *Papaver somniferum* grown in darkness germinated in the usual manner. I am constrained to call attention to the fact that these results have not been confirmed by Amelung, who carried out a similar series of tests in 1894. The general relations of light to form and growth were considered in later papers by Sachs, and without further discussion of his lengthly dissertations the chief conclusions may be briefly stated as follows :

Light is not necessary for cell-division of non-green organs, but is indispensable for organs containing chlorophyl.

Exaggerated elongation of internodes is accomplished by increased extension of the cells, not by multiplication of cells.

The chief purpose of stems is to carry buds aloft to sunlight, and most stems form greatly elongated internodes when etiolated ; to this may be noted the exceptions which fall into two groups. One includes plants with long slender internodes supposed to be normally etiolated, and the other with compressed internodes which exhibit no capacity for elongation.[32]

The development or non-development of flowers in darkness was held to be dependent upon the presence of the special nutritive substances necessary for their growth.

Plants with adequate supplies of special reserve material might form normal flowers in darkness, but plants devoid of such reserve material might perfect flowers only when a branch or leafy stem was exposed to the light and could furnish the necessary constructive material.

The term *photolonus* was applied to the condition of the plant when receiving illumination of a certain intensity sufficient to induce a labile condition of the protoplasm. Under such conditions the plant might accomplish normal growth, food formation and development.

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[32] Sachs. Ueber den Einfluss der Lufttemperatur und des Tageslichts auf die stündlichen und täglichen Aenderungen des Längenwachstums (Streckung) der Internodien. Arb. a. d. Bot. Inst. i. Würzburg, **1** : 99. 1872.

Sachs. Vorlesungen ueber Pflanzenphysiologie. 1865.

Sachs. Wirkung farbigen Lichts auf Pflanzen. Bot. Zeitung, **22** : 353, 361, 369. 1864.

Sachs. Ueber die Wirkung der ultravioletten Strahlen auf die Blüthenbildung. Arb. a. d. Bot. Inst. i. Würzburg, **3** : 372. 1887.

Sachs. Gesammelte Abhandlungen ueber Pflanzenphysiologie, **1**: 229, 261. 1892.

Darkness-rigor was used to denote the stable and non-motile condition of protoplasm after continued deprivation of illumination, under which circumstances all periodic movements and other activities were said to cease.

Variations in intensities of illumination were supposed to induce the assumption of day and night positions of leaves, and other organs in a phototonic condition, by the paratonic action of the rays. Leaves and internodes which have grown under normal alternations of day and night grow more slowly in temporary illumination than in darkness, due to the retarding action of light.

Etiolation is a pathological condition, and the diminished stature of leaves is due to defective nutrition, and not to lack of illumination alone.

Only chlorophyl-bearing organs might be etiolated ; floral organs, customarily free from chlorophyl, fruits and seeds, may develop in a fairly normal manner in darkness.

It is notable that the investigations of Sachs and the workers in his laboratory resulted in the record of an enormous number of facts concerning growth and the relation of light to plants, and that these researches led the way to nearly all of the modern work upon the subject, yet scarcely a single one of his conclusions concerning etiolation, and the influence of light upon growth are tenable at the present time except in modified form. Some of his imperfect interpretations must have been due to a failure to comprehend the bearing of the reactions of fungi to light and darkness.

G. Kraus'[33] conclusions published in 1869 ascribed the undeveloped stature of etiolated leaves to a lack of nutrition, upon the supposition that leaves were dependent upon the products of their own chlorophyl apparatus for food. The excessive elongation of etiolated stems was supposed by Kraus to be due in part to a slight multiplication of the cells, and to an exaggerated elongation of these elements. Stress was laid upon the predominating influence of turgid parenchyma cells as a positive factor in such stretching. The walls of the fundamental system were seen to remain unthickened for a month or more, in etiolated stems. Torsions were found in all hypocotyls, but were not analogous to the torsions of climbing stems, being produced directly by the inclined position and prosenchymatous form of the epidermal cells. Later some important investigations were made by Kraus upon the water content of plants in light and darkness in which he found that etiolated plants showed a greater percentage of water in their composition. The exclusion of light from a plant was followed by a swelling due to an increase of the amount of water present, and the actual size of the plant showed fluctuations during the day, which were more or less irregular. The acidity of the sap of plants were observed to increase in darkness for the most part, and in many instances the acidity of etiolated plants was greater than that of normal specimens.[34]

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[33] Kraus, G. Ueber die Ursachen der Formänderungen etiolirender Pflanzen. Jahrb. Wiss. Bot. 7: 209. 1869.

Kraus completed some experiments upon the influence of partial spectra upon plants in 1876, from which he reported that excessive elongation of aërial roots and stems in *Mimosa* and *Urtica dioica* occurs in red and yellow light as in darkness. *Mimosa* did not go into a condition of darkness rigor in yellow light and soon recovered from darkness rigor when placed in yellow light. This plant was found to go into darkness rigor in green light in confirmation of earlier results by Bert.[35]

Batalin[36] wrote two contributions upon this subject in 1869 and 1871. His earlier work was directed toward a study of the influence of light upon the separate tissues, and may be best stated in an adaptation of his own summary. Light exercises no influence upon the division of epidermal cells, as illustrated by observations on *Lepidium sativum*. Diffuse light facilitates division of the cortical parenchyma (*Lepidium sativum*), and direct sunlight exercises the same effect on these cells as darkness. Light acts favorably on the formation of woody tissue (*Cannabis sativa*, *Zea Mais*), and the formation of secondary bundles is facilitated by light (*Triticum vulgare*, *Zea Mais*). Collenchymatous thickening is carried on only to a limited extent in darkness (*Solanum tuberosum*), while the thickening of the walls of bast and wood cells is not affected by light. Not all of these results are confirmed by later investigations.

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[34] Kraus. Ueber die Wasservertheilung in der Pflanze. I. Halle. 1879. III. Die tägliche Schwellungsperiode der Pflanze. 1881. IV. Die Acidität des Zellsaftes 1884.

[35] Kraus, G. Versuche mit Pflanzen im farbigen Licht. Abdruck a. d. Sitzungsber. d. Naturf. Ges. z. Halle. 1876.

[36] Batalin, A. Ueber die Wirkung des Lichtes auf das Gewebe einiger mono- und dicotyledoner Pflanzen. Bull. d. l. Acad. Imp. d. St. Petersbourg, 7: 269. 1869.

Later Batalin[37] combated the self-nutrition of leaves as formulated by Kraus, and held that chlorophyl plays no direct part in the development of the leaf, this organ being able to carry on growth as long as it was furnished food. He upheld his former contention that the small size of etiolated leaves is due to their inability to carry on cell division in darkness. He also called attention to the mistaken statement of Weiss[38] that etiolated leaves have the same number of stomata as normal leaves.

Famintzin[39] carried out some experiments in an effort to analyze the growth of algae in light and darkness, and found that cell-division ensued almost wholly in light. His claim that this relation of light to division is not due to nutritive conditions, rests chiefly upon a series of tests in which filaments of *Spirogyra* were exposed to light until the cells were loaded with starch, then some were continued in light and others were placed in darkness. In such instances the greatest multiplication was shown by the illuminated filaments. Karsten's[40] tests showed a greater proportion of cellulose in etiolated specimens than in the normal, or an actual amount about equal to the normal.

Prantl[41] investigated the relation of light to growth in Sach's laboratory and by measurement of the number and size of cells in etiolated, and embryonic normal leaves, concluded that cell division does ensue in etiolated organs of this character. In addition to a re-statement of some of Sachs' conclusions regarding influence of light upon growth, he also repeats the assertion of Sachs that etiolated leaves are in a pathological condition, due to the lack of the specific substances necessary for their proper nutrition.

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[37] Batalin, A. Ueber die Wirkung des Lichtes auf die Entwickelung der Blätter. Bot. Zeitung, 29: 669. 1871.

[38] Weiss, A. Untersuchungen ueber die Zahlen und Grössenverhältnisse der Spaltöffnungen. Jahrb. f. Wiss. Bot. 4: 125. 1865–1866.

[39] Famintzin, A. Die Wirkung des Lichtes auf Algen und einige andere ihnen nahe verwandte Organismen. Jahrb. f. wiss. Bot. 6: 1. 1867.

Famintzin, A. Die Wirkung des Lichts auf das Wachsen keimenden Kresse. Mem. Acad. St. Petersb. 8: p. 13. No. 15. 1865.

[40] Karsten, H. Vergleichenden Untersuchungen von in Lichte und Dunkeln gezogenen Pflanzen. Der Chem. Ackersman. No. 3. 1870.

Karsten, H. Die Einwirkung des Lichtes auf das Wachstum der Pflanzen beobachtet bei Keimung der Schminkbohnen. Inaug. Diss. Jena. 1870.

[41] Prantl, K. Ueber den Einfluss des Lichtes auf das Wachstum der Blätter. Arb. a. d. Bot. Inst. Würzburg, 1: 371. 1873.

As early as 1873 Godlewsky[42] maintained that the form of etiolated leaves was not due to lack of nutrition, and as will be shown later, he consistently progressed in the development of a theory of etiolation as an adaptation.

Detmer[43] investigated the influence of varying intensities of light upon the elongation, turgidity and composition of etiolated shoots. The amount of elongation shown by stems was found to increase with the diminishing intensity of illumination, and was ascribed to the "great turgor extension of the cells," while the expansion of the leaves decreased under the same circumstances. The percentage of dry matter in shoots was lessened as the intensity of the illumination diminished.

In a later research it was observed that etiolated seedlings of *Cucurbita* held the cotyledons in an erect position with the inner surfaces appressed. An exposure to light would bring these organs down to the normal horizontal position. As a result of this and similar observations Detmer concluded that light directly affected the relative rapidity of growth of the sides of a dorsiventral organ, and he used the terms *photo-epinasty* and *photo-hyponasty* to designate such relation.[44]

Lasareff[45] believed he had established a correlation between the length of the stem and the extent of the root-system in etiolated plants in confirmation of some results obtained by Famintzin. The total length of the roots of a number of common forms decreased as the length of the stem increased, in etiolated series, and secondary roots were shorter and fewer.

Strehl[46] made a series of measurements of the roots and hypocotyls of *Lupinus albus*, by which it appeared that those grown in darkness attained much greater lengths than those under ordinary conditions. These experiments did not clearly demonstrate the retarding influences of light, however. This is also true of von Wolkoff's measurements as described by Sachs.[47]

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[42] Godlewsky, E. Abhängigkeit der Stärkebildung in den Chlorophyllkörnern von den Kohlensäuregehalt der Luft. Flora, **56**: 378. 1873.

[43] Detmer, W. Ueber den Einfluss verschiedener Lichtintensitäten auf die Entwickelung einiger Pflanzen. Landw. Versuchss. **16**: 205. 1873. See also Detmer, Practical Plant Physiology. Pp. 404–411. 1898, and Detmer, Vergleichende Physiologie d. Keimungsprocesses d. Samen. 1880.

[44] Detmer, W. Ueber Photoepinastie der Blätter. Bot. Zeitung. **40**: 787. 1882.

[45] Lasareff, N. Ueber die Wirkung des Etiolirens auf die Form der Stengel. Beil. z. Protocoll d. 45th Sitzung. d. Naturf. Ges. a. d. Univ. z. Kasan. Abstract in Bot. Jahresber. **2**: 775. 1874.

[46] Strehl, R. Untersuchungen über das Längenwachstum der Wurzel und des hypokotylen Glied. 1874.

Koch's[48] examinations of etiolated stems of cereals revealed the imperfect development of certain tissues of mechanical value which resulted in the "laying" of plants when grown too closely crowded. Decrease of illumination was found to cause an exaggerated extension of stems due to the greater elongation of their components, and was accompanied by an attainment of a diameter below the normal. Such changes ensued only in organs treated while in the earlier stages of growth and as these alterations rested upon the action of existing cells rather than upon the formation of new elements, the elongation was greatest in the basal portions of internodes. Less thickening ensued in the walls of such elongated elements but lignification proceeded in the customary manner.

In some investigations of the relation of light to the construction and disintegration of chlorophyl, Wiesner[49] found that this substance might originate in an etiolated specimen in an illumination too faint to be discerned by the eye, a fact of great importance in imperfect etiolation. Disintegration ensued only when light of sufficient intensity to cause food formation was allowed to act upon the plant. The formation of chlorophyl in etiolated plants ensued most quickly in rays passing through a solution of cupric ammonia.

The self-nutrition theory of G. Kraus and others was affirmed by C. Kraus in some publications in 1875,[50] and he also concurred in the theory of Sachs that light retards growth by its direct action. Later C. Kraus attempted a refutation of the principal results of Godlewsky's earlier researches.

Walz[51] performed a series of tests of wide inclusiveness in 1875 in which it was confirmed that spores of ferns and oöspores of

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[47] Sachs. Text Book of Botany, 2d Ed., p. 835.

[48] Koch. Abnorme Aenderungen wachsender Pflanzenorgane durch Beschattung. Berlin 1872.

[49] Wiesner, J. Vorläufige Mittheilung über den Einfluss des Lichtes auf Entstehung und Zerstörung des Chlorophylls. Bot. Zeitung, 32: 116. 1874.

[50] Kraus, C. Pflanzenphysiologischen Untersuchungen. VI. Wachstum und Chlorophyllbildung. Flora, 58: 346. 1875.

Kraus, C. Ursachen der Formänderung etiolirter Pflanzen. Bot. Zeitung, 37: 332. 1879.

[51] Walz, J. W. Ueber die Wirkung des Lichtes auf einige Processe des Pflanzenlebens. Schrift. d. k. Neuruss. Univ. i. Odessa, 17: —. 1875. Abstract in Bot. Jahresber. 3: 786. 1875.

Vaucheria sessilis germinating in darkness produced chlorophyl. *Amaryllis formosissima* produced normal flowers in darkness but with altered colorations. The length and thickness of roots of etiolated plants was less than those grown in light. The total length of the roots of an etiolated *Phaseolus vulgare* was 700 mm. Total length of illumined roots with etiolated shoot 1,254 mm. Total length of root system with entire plant illumined 6,276 mm. Total length of root system with illumined shoot and darkened roots, 3,256 mm. These measurements were made on plants grown in water cultures. The roots of an etiolated specimen of *Helianthus annuus* measured 974 mm., and in an example with etiolated shoot and illumined roots the latter gave a total measurement of 1,252 mm.

Mer[52] found a correlation existed among the members of the shoot by reason of which the excessive elongation of one was accompanied by the lessened growth of others. He concluded that plants with a basipetal mode of development were unable to extend these organs to their normal position. Internodes and petioles become longer in darkness by reason of lessened tissue tensions. The shortness and non-development of branches and other organs was attributed to lack of nutrition.

Rzentkowsky[53] reported similar correlations expressed in terms of rate of growth. He also found that etiolated plants take up less mineral matter than normal ones, a fact probably resultant from the lessened transpiration.

Borodin[54] estimated the respiration of branches of *Crataegus monogyna* and *Spiraea opulifolia* in darkness and found that the quantity of carbon dioxide exhaled was much increased during the period immediately following deprivation of light. Twelve hours later the rate of liberation of this gas had decreased to half the normal, and 24 hours later to one third. The normal rate was quickly resumed when illumination was restored, presumably due to the formation of material available in respiration, according to the author.

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[52] Mer, E. Recherches sur les anomalies de dimensions des entre-noeuds et de feuilles étiolées. Bull. Bot. Soc. d. France, 22: 190. 1875.

[53] Rzentkowsky, T. Untersuchung über die Entwickelung des etiolirten *Phaseolus multiflorus*. Mitth. a. d. Univ. z. Warschau. Abstract in Bot. Jahresber. 4: 745. 1876.

[54] Borodin, J. Physiologischer Untersuchung über die Athmung der beblätterten Sprosse. Arb. d. St. Petersb. Ges. d. Naturf. 7: 1–114. 1876. Abstract in Bot. Jahresber. 4: 919. 1876.

A continuation of the etiolation of inflorescences after Sachs' method was undertaken by Askenasy,[55] who found that flowers of *Hyacinthus orientalis*, *Scilla campanulata*, *Pulmonaria officinalis*, *Orchis ustulata*, *Silene pedula*, *Antirrhinum majus*, *Digitalis purpurea* and *Prunella grandiflora* did not exhibit the normal color scheme. Not only were green floral envelopes blanched, but variations in the depth of other pigmentated areas were observable.

Heckel[56] believed he had demonstrated that certain organs, which were normally irritable to contact, went into a condition of rigor in darkness, an observation that could not be confirmed by Pfeffer.

Baranetzky[57] investigated the relation of the rate of growth to darkness and illumination with the result that he concluded that the daily periodicity in growth was not due directly to the alternating periods of illumination and darkness, but was an after effect. Thus plants exhibiting daily periodicity in the rate of growth did so on several successive days when placed in darkness, and after the rhythm was lost in darkness it was again taken up after exposure to illumination for twelve hours.

Brefeld[58] observed that the growth and development of fungi is more or less dependent upon light, and that sporophores of many fungi exhibited excessive elongation in darkness. The sporophore of *Pilobolus microsporus* attained a length of half an inch in light and of 8 to 10 inches in darkness.

Schulzer von Muggenburg reported a number of collected observations concerning the relations of fungi to light which are in harmony with Brefeld's results.[59] A large number of notices showing that different species of fungi exhibit the most diverse reactions to the presence and absence of light were published between 1875 and

[55] Askenasy, E. Ueber den Einfluss des Lichtes auf die Farbe der Blüthen. Bot. Zeitung, **34**: 1, 27. 1876.

[56] Heckel, E. Du mouvement végétal. Paris. 1875. Review by Pfeffer in Bot. Zeitung, **34**: 9. 1876.

[57] Baranetzky, J. Die selbstständige tägliche Periodicität im Längenwachstum der Internodien. Bot. Zeitung, **35**: 639. 1877.

[58] Brefeld. Ueber die Bedeutung des Lichtes für die Entwickelung der Pilze. Bot. Zeitung, **35**: 386. 1877. Also, Sitzungsber. d. Ges. Naturf. z. Berlin. April. 1877.

[59] Schulzer von Muggenburg. Des allelebenden Lichtes Einfluss auf die Pilzwelt. Flora, **61**: 119. 1878.

1890, to which no reference will be made here; a full discussion is given in the monographs of Elfving and Grantz.[60]

Rauwenhoff[61] made extensive investigations of the relations of light to form, and development of tissues, a preliminary notice of which was published in 1876 and the full account in 1878. He concluded that not only the pith but the entire fundamental tissue participated as active factors in the excessive lengthening of stems. He regarded the theories of Kraus and also of Batalin regarding the small size of etiolated cotyledons as untenable. The lack of thickening of walls, and the non-development of the wood and sheath in the fibrovascular bundles was noted. The theories of the correlation existing between the root and shoot by which the former showed a decreased development in etiolated specimens were not confirmed. Rauwenhoff concluded that leaves exhibiting marked dorsiventrality were most likely to remain small in etiolation. The anomalous structures of etiolated plants were ascribed to the action of negative geotropism, unhindered by heliotropism. Lastly Rauwenhoff regarded etiolation as a pathological phenomenon.

Stebler[62] attempted a refutation of the theory of Sachs as the universal prevalence of a daily periodicity of growth. Stebler accepted the conclusion that light may retard growth, but found that the greatest increase in monocotyledonous leaves occurred during the most intense illumination, and that this growth is intimately connected with food-formation. Such daily maxima also occurred at a corresponding part of the middle of the day in etiolated specimens. Dicotyledonous leaves exhibited the most rapid growth in the middle of the forenoon, which continued until the favorable influence of rapid food-formation was counterbalanced by the retarding influence of light. The decreased and decreasing rate continued until the following morning when assimilation was again resumed. The difference in the behavior of the two forms of leaves was due to the location of the growing region, which is basal in the linear monocotyledonous type and is shielded from the direct action of the rays.

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[60] Elfving, F. Studien ueber die Einwirkung des Lichts auf die Pilze. Helsingfors. 1890.

Grantz, F. Ueber den Einfluss des Lichtes auf die Entwickelung einiger Pilze. Leipzig. 1898.

[61] Rauwenhoff, N. W. P. Sur les causes des formes anormales des plantes. Ann. Sc. Nat. VI. 5 : 267. 1878.

[62] Stebler, F. G. Untersuchungen über das Blattwachstum. Jahrb. f. Wiss. Bot. 11 : 47. 1878.

Another attempt to establish a correlation among the members of the shoot and root systems was made by C. Kraus[63] in 1878. He believed he had demonstrated that the smallness of etiolated leaves was caused directly by the excessive elongation of the internodes and the increased length of the shoot was accompanied by a similar decrease in the root-sysem. These measurements were thought to be correspondent to the degree of turgidity exhibited by the organs concerned.

Vines[64] made two series of experiments to ascertain the direct relation of light to growth in 1878, at the laboratories in Würzburg. Partial spectra and atmospheres lacking carbon dioxide were used in some of the tests. From direct measurements of the rate of elongation of sporophores of *Phycomyces* in darkness and light, and in various portions of the spectrum he concluded that light retards growth by the direct action of the blue-violet rays, and this effect was supposed to be due to a decrease in the mobility of the micellae of the peripheral layers of protoplasm. These conclusions, as well as the more important generalizations made by Sachs, are given by Vines in his text-books of plant physiology and botany and do not need further description here.

Godlewsky[65] took up the subject for the second time in 1879 and his principal results may be stated as follows: The organic material in an etiolated seedling, and in one grown in atmosphere lacking carbon dioxide is not greater than the amount present in the seed, and is approximately equal in the two instances. The altered form of the stem and cotyledon is not due to altered assimilation. The total amount of dry material in cotyledons of etiolated seedlings of *Raphanus* is less than in green ones. Roots of etiolated plants may be slightly less developed than in the normal, yet no regular correlation appears between the root and shoot in this connection.

[63] Kraus, C. Ueber einige Beziehungen des Lichtes zur Form und Stoffbildung der Pflanzen. Flora, **61**: 145. 1878.

[64] Vines, S. H. The Influence of Light upon the Growth of Leaves. Arb. a. d. Bot. Inst. i. Würzburg, **2**: 114. 1878.

Vines, S. H. The Influence of Light upon the Growth of Unicellular Organs. Arb. a. d. Bot. Inst. i. Würzburg, **2**: 133. 1878.

Vines, S. H. Physiology of Plants. 1886, and Student's Text-book of Botany. 1896.

[65] Godlewsky, E. Zur Kenntniss der Ursachen der Formänderung etiolirter Pflanzen. Bot. Zeitung, **37**: 81, 97, 113, 137. 1879.

According to Wiesner's[66] investigations etiolated seedlings are capable of much more delicate phototropic reactions than others grown in diffuse light. He also believed to have confirmed the conclusion that light retards growth, finding that such effect was exercised even by intensities insufficient to act as phototropic stimuli. The retarding effect was attributed to the entire spectrum, and was quite as great in intense yellow as in blue light. The retarding influence of light was ascribed to the action of the rays not only on the peripheral layers of protoplasm, but also on the wall, as well as upon turgidity.

A decade later Godlewsky[67] reviewed the entire subject and, after a masterly discussion of the established facts of etiolation, concluded that the theories of self-nutrition and that etiolation was a pathological phenomenon, were inadequate. He proposed instead that such reactions were purely adaptive in their nature and are designed to bring the reproductive and food forming organs up into light as rapidly as possible, the food and energy of the plant being directed to the development of the members which would accomplish this purpose. The same theory had been proposed in a general form by Boehm[68] three years previously.

In some later investigations by Godlewsky plants kept in darkness until 11 A. M. were found to exhibit a minimum rate at 9 A. M., and after illumination at 11 A. M. the rate was below the normal. The elongating zones were found to be longer in etiolated than in normal green plants, but the turgidity was no greater. Godlewsky affirms that the ductility of etiolated and normal stems is about the same. Maximum ductility in any given cell is maintained longer in etiolated plants however. The illumination of an etiolated plant is followed by a decrease of ductility and elasticity of the older cells of the growing zone. Light was supposed to check the superficial expansion of growing cells, and retard elongation.

[66] Wiesner, J. Die heliotropischen Erscheinungen im Pflanzenreiche. II. Th. 7. 1880.

[67] Godlewsky, E. Ueber die biologische Bedeutung der Etiolirungserscheinungen. Biol. Centralblatt, 9: 481. 1889.

Godlewsky, E. Ueber die Beeinflussung des Wachstums der Pflanzen durch aeussere Factoren. Anzeig. d. Akad. d. Wiss. z. Krakau. Résumés, p. 206. 1890.

Godlewsky, E. Die Art und Weise der Wachstumsretardirenden Lichtwirkung und die Wachstumstheorien. Anzeig. d. Akad. d. Wiss. z. Krakau. Résumés, p. 166. 1890.

[68] Boehm. Die Nahrstoffe der Pflanze. 1886.

An interesting example of excessive elongation due to etiolation is given by Krabbe[69] who records that the apothecial stalks of *Baeomyces* attain a length much beyond the normal when deprived of illumination.

Vöchting[70] found that light exerted a strong selective influence in the development of shoots ; only the buds favorably acted upon by light showed activity in the formation of branches. Later a reverse instance of this action was seen in the potato in which tubers were formed only on organs deprived of illumination. Vöchting has carried out a large number of researches which bear directly and indirectly upon this subject. He found that leaves of etiolated plants brought into light in an atmosphere lacking carbon dioxide did not form chlorophyl, and hence concluded that the growth of these organs is intimately connected with their food-forming operations. Later he also found that the formation of flowers is closely connected with the activity of the leaves, in addition to which light exerts a direct morphogenic effect upon these structures. Diverse reactions were recorded in which some flowers were seen not to open in darkness or diffuse light, while others opened but did not reach normal stature. Light also exerted various effects upon the essential parts of the flower. As a result of a series of etiolations of cacti it was found that the form of these plants is largely dependent upon illumination, and that deprivation of light acts as a stimulus which calls out renewed growth.

Noll[71] relates that etiolated twining plants were capable of grasping supports in the usual manner, such action being ascribed to negative geotropism and circumnutation, an experience that has been duplicated by no other worker on this subject so far as the records are available.

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[69] Krabbe, G. Entwickelung, Sprossung und Theilung einiger Flechten Apothecien. Bot. Zeitung, 40 : 93. 1882.

[70] Vöchting, H. Organbildung im Pflanzenreich, 2 : 66. 1884.

Vöchting, H. Ueber der Knollenbildung. Bibl. Botan. 1 : Hft. 4. 1887.

Vöchting, H. Ueber die Abhängigkeit des Laubblattes von seiner Assimilationsthätigkeit. Bot. Zeitung. 49 : 113. 1891.

Vöchting, H. Ueber den Einfluss des Lichtes auf die Gestaltung und Anlage der Blüthen. Jahrb. f. Wiss. Bot. 25: 149. 1893.

Vöchting, H. Ueber die Bedeutung des Lichtes für die Gestaltung blattförmiger Cacteen. Zur Theorie der Blattsteilungen. Jahrb. f. wiss. Bot. 26 : 438. 1894.

Vöchting, H. Zur Physiologie der Knollenge wächse. Jahrb. f. Wiss. Bot. 34 : 1. 1900.

See also, Istvanffi, G. Influence of Light upon the Development of Flowers. 1890.

[71] Noll, F. Ueber rotirenden Nutation an etiolirenden Keimpflanzen. Bot. Zeitung. 43 : 664. 1885.

Klein[72] made a series of experiments to determine the factors to which the nocturnal spore formation of *Botrytis cinerea* might be ascribed, and concluded that the blue violet rays exerted such direct action as to prevent their production during the daytime. The red-yellow rays facilitated spore formation, and the absence of light allowed it to proceed normally.

The etiolation of a number of such extremely hairy forms as *Urticula pilulifera*, *Cynoglossum officinale*, *Anchusa officinalis*, *Cucurbita Melopepo*, *Ecballium elaterium*, *Soja hispida*, *Salvia argentea*, *Stachys lanata*, *Mirabilis Jalapa*, *Abutilon Avicennae*, *Gloxinia hybrida*, *Solanum tuberosum*, *Dahlia variabilis*, *Mentha piperita* and *M. crispa*, by Schober[73] resulted only in the diminution of the size of the trichomes, or excessive growth correspondent to that of the organs on which they are borne. The stellate hairs of *Abutilon* were not borne by etiolated specimens. The above results must be accepted with some caution, however, since etiolations were affected by covering shoots with flower pots and could hardly have been absolute.

As a result of some researches upon the structure of leaves Dufour[74] concluded that these organs reached a greater extension in sunlight than in shade, that the epidermal cells were larger, the number of stomata greater and that a continued formation of these organs ensued occurred through a large part of the period of development of the leaf. Stahl[75] had previously published the results of his extensive researches upon the general relations of the form and size of leaves to light exposure and other factors.

Uhlitzsch[76] showed that the extension of petioles is greater in etiolated than normal leaves, but that growth may be variously affected by light in different species. The length of the period of growth is also dependent upon the intensity of the illumination.

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[72] Klein, L. Ueber die Ursachen der ausschliesslich nächtlichen Sporenbildung von *Botrytis cinerea*. Bot. Zeitung, **43**: 6. 1885.

[73] Schober, A. Ueber das Wachstum der Pflanzenhaare an etiolirten Blatt- und Achsenorganen. Zeitschr. f. Naturw. IV. **58**: 4: 556. Abstract in Bot. Centralb. **28**: 39. 1886.

[74] Dufour, L. Influence de la lumière sur la structure des feuilles. Bull. Bot. Soc. d. France, II. **8**: 92. 1886.

[75] Stahl, E. Ueber die Einfluss des Standortes auf die Ausbildung der Laubblätter. 1883.

[76] Uhlitzsch, P. G. Untersuchungen über das Wachstum der Blattstiele. 1887.

Vines[77] examined Detmer's conclusions as to photo-epinasty and photo-hyponasty and demonstrated that such movements are spontaneous, and not induced, though occurring under certain intensities of illumination. It was asserted that the above terms might only be properly applied to adaptive movements, such as those in which the leaf assumes a vertical position in consequence of unfavorable intensities of illumination.

In an attempt to make an orderly classification of the fungi numerous observations of variations in form have been made as far back as the latter part of the eighteenth century. A few of these observations have been noted on the previous pages, and a thorough bibliographical account of this aspect of the subject was published by Elfving,[78] in 1890. Elfving concluded that light retarded many of the synthetic processes of fungi, though not all of them, and that the ultra-violet as well as the visible rays participated in such action. Similar influence was exerted upon respiration. Diffuse light had effects similar to darkness and diverse reactions were exhibited by various species.

Busch made a number of systematic tests of the endurance and development of green plants in darkness in 1889, the principal result of interest in this connection being that fruits not normally containing much chlorophyl might attain normal development in darkness if the leaves were illuminated.[79]

Recent researches tend to show that light has but little influence upon respiration, yet some notable differences are found between the respiration of etiolated and normal plants. Much work upon this phase of the subject has been done by Palladine,[80] who concluded that the respiratory activity of etiolated shoots is considerably augmented by the introduction of sugar into the tissues. The respiratory quotient of etiolated leaves varies from .72 to .76, in a water culture, it ranges from .63 to .65 and in a culture of sugar about .76. The respiratory activity of both normal and etiolated leaves decreases after confinement in darkness for prolonged periods.

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[77] Vines, S. H. On Epinasty and Hyponasty. Annals of Botany, 3: 415. 1889.

[78] Elfving. Studien über die Einwirkung des Lichtes auf die Pilze. 1890.

[79] Busch, H. Untersuchungen ueber die Frage ob das Licht zu den immittelbaren Lebensbedingungen der Pflanzen oder einzelner Pflanzenorgane gehört. Inaug. Diss. Bremen. 1889.

[80] Palladine, W. Transpiration als Ursache der Formänderung etiolirter Pflanzen. Ber. d. Deut. Bot. Ges. 8: 364. 1890.

Palladine, W. Eiweissgehalt der grünen und etiolirten Blätter. Ber. d. Deut. Bot. Ges. 9: 194. 1891.

Palladine, W. Ergrünen und Wachstum der etiolirten Blätter. Ber. d. Deut. Bot. Ges. 9: 229. 1891.

Palladine, W. Recherches sur la respiration des feuilles vertes et des feuilles étiolées. Rev. Gen. d. Bot. 5: 449. 1893.

Palladine saw in the form of etiolated plants a direct adaptation to the altered transpiratory conditions resulting chiefly from the absence of light, and points out that the anatomy of etiolated stems is much like that of stems grown in chambers with a saturated atmosphere. A chemical analysis of etiolated plants showed them to be capable of division into two groups. One group, including the stemless plants contains less proteids than green organs, and the second includes plants with stems, the leaves of which contain more proteid than the normal, while the stems are depleted of this substance.

In some experiments upon the formation of green color and growth with separated etiolated leaves, Palladine found that the formation of chlorophyl in etiolated leaves is accomplished only when a supply of sugar is at hand, and that lack of calcium will prevent the development of leaves of *Vicia Faba*.

Lamarlière[81] concluded that the differences in the structure of leaves in diffuse light from those in direct sunlight corresponded directly to the diminished functions of respiration, food-formation and transpiration in the former instance.

C. DeCandolle repeated the experiments of Sachs in testing the influence of the ultra-violet rays, and his results partly confirmed the conclusions of Sachs that these rays are necessary for the construction of specific substances used in the formation and growth of floral organs. The rays in question were excluded from the plants by solutions of quinine and aesculine, and since some flowers were formed on the screened plants a stimulative action of the ultra-violet rays was suggested.[82]

Frank[83] recognized the futility of attempts to make generalizations on the influence of light upon growth in his text-book in 1892, and concluded that etiolation phenomena are exhibited only by organs, the activity of which is concerned with the sun's rays. He saw in etiolation an effort to carry organs up to sunlight to the functions of which the radiations were necessary. His view is practically that of Godlewsky, although he makes no mention of the latter among the references made to other writers.

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[81] De Lamarlière, L. G. Recherches physiologiques sur les feuilles dévellopées a l'ombre et au soleil. Rev. Gen. d. Bot. 4: 481. 1892.

[82] DeCandolle, C. Etude de l'action des rayons ultra-violet sur la formation des fleurs. Arch. des Sc. Phys. et Nat. Genève, 28: 265–277. 1892.

[83] Frank, B. Lehrbuch der Botanik, 1: 389. 1892.

Wiesner made a quantitative examination of the influence of illumination of various intensities in producing etiolative effects and in causing alterations of stature. Leaves and stems were found to respond unequally to such variations.[84]

Ziegebein[85] also found that etiolated shoots of *Solanum* respired less actively than normal stems.

Among other reactions of aquatic plants those shown by *Caulerpa* are strikingly similar to those of the higher plants, according to the observations of Klemm,[86] Noll[87] and Berthold.[88] No foliar prolifications are produced by specimens grown in darkness and the small number of branches sent out take the form of cylindrical bodies entirely free from chlorophyl.

Godlewsky[89] again attacked the problem of daily variations in the rate of growth and found that daily periodicity might or might not be exhibited. A sudden illumination of a plant which has been kept in darkness for several hours causes a diminution of the rate of growth in a very short time. The decrease continues for 1½ to 4½ hours then slowly regains the original rate, consequently he held that the daily periodicity was due to the direct influence of light.

Frankfurt[90] made an extensive series of analyses of the composition of seeds and etiolated seedlings of *Cannabis sativa* and *Helianthus annuus* in 1893. Attention was directed chiefly to the estimation of asparagin and glutamin in the first species. Seedlings of *Helianthus* 12 days old were found to be rich in soluble carbohydrates, poor in nitrogenous bases, to contain no starch, some pentosanes, and an increased amount of simple nitrogen compounds of organic acids and hemicelluloses.

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[84] Wiesner, J. Photometrischen Untersuchungen auf Pflanzenphysiologischen Gebiete. Sitzungsber. d. Kaiserl. Akad. d. Wiss. i. Wien. 102 : Abth. 1. 1893.

[85] Ziegebein, E. Untersuchungen über den Athmung keimende Kartoffelknollen sowie anderer Pflanzen. Jahrb. f. Wiss. Bot. **25** : 563. 1893.

[86] Klemm, P. Ueber *Caulerpa prolifera*. Flora, 77 : 460. 1893.

[87] Noll, F. Ueber die Einfluss der Lage auf die morphologische Ausbildung einiger Siphoneen. Arb. a. d. Bot. Inst. i. Wurzburg, **3** : 466. 1888.

[88] Berthold, G. Beiträge zur Morphologie und Physiologie der Meeresalgen. Jahrb. f. Wiss. Bot. **13** : 569. 1882.

[89] Godlewsky, E. Studien über das Wachstum der Pflanzen. Abh. d. Krakauer Akad. d. Wiss. Math.-Naturw. Cl. **23** : 1–157. Abstract by Rothert. Bot. Centralbl. **55** : 34. 1893.

[90] Frankfurt, S. Ueber die Zusammensetzung der Samen und etiolirten Keimpflanzen. Inaug. Diss. Wilna. 1893.

A number of etiolation experiments by Jost[91] with buds of trees gave the result that the development of such buds was hindered by darkness in the case of the copper beech. On the other hand firs, rhododendron, horse chestnut and maple developed long thin etiolated shoots, which soon perished, except in the case of the horse chestnut. In the last-named tree closed winter buds were formed after the etiolated stems had reached a certain length, which perished after another attempt at growth. Only a few buds awoke on an entire plant of copper beech placed in the dark room, affording an example exactly opposite that of the potato.

In a second series of tests Jost made a careful examination of the irritable condition of etiolated plants, in which *Mimosa*, *Phaseolus* and other species were used. *Mimosa* exhibited its usual capacity for reaction to shock, wounds and other stimuli, and carried on periodic movements in a rhythm fairly correspondent to that in daylight. The atrophied form of etiolated leaves was asserted to be due to lack of nutrition, since rudimentary leaves freed from the competition of concurrent organs arising from the same bud or branch attained normal extension and stature. The death of green leaves in darkness was attributed to the pathological effects of disintegrating chlorophyl.[92]

Amelung[93] repeated Sachs' experiment with etiolation of tips of stems of *Cucurbita* and the flowers produced differed much from the normal. Some of them did not open, and fertilization was accomplished only by the introduction of pollen grown on plants in the open air. A fruit was formed in darkness as the result of such pollination, which showed various divergences from the normal, as well as the seeds which were not capable of germination.

Goebel[94] pointed out that some of the reactions of etiolated plants, or of plants in diffuse light are correlation phenomena, or adaptive processes and are not due to the direct effect of illumination or the lack of it, a supposition parallel to and corroborative of the theory of Godlewsky. Goebel's general discussion of the subject in his Organography will be considered in a later section of this memoir.

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[91] Jost, L. Ueber den Einfluss des Lichtes auf das Knospentreiben der Rothbuche. Ber. d. Deut. Bot. Ges. **12**: 188. 1894.

[92] Jost, L. Ueber die Abhängigkeit des Laubblattes von seiner Assimilationsthätigkeit. Jahrb. f. Wiss. Bot. **27**: 403. 1895.

[93] Amelung, E. Ueber Etiolement. Flora, **78**: 204. 1894.

[94] Goebel, K. Ueber die Einwirkung des Lichtes auf die Gestaltung der Kakteen und anderer Pflanze. Flora, **80**: 96. 1895.

Klemm[95] concluded that light is not necessary for the existence of protoplasm, and a certain maximum intensity acts unfavorably and fatally, producing granulation and rigor, but not vacuolization. Such action is not so marked as with heat radiations, however.

The behavior of aquatic plants in darkness offers some interesting data, especially those offered by the seed-plants. Möbius[96] found that *Ceratophyllum* showed excessive elongation of its internodes, and placed the leaves in a drooping position, as well as the branches. The excessive length of the internodes was correspondent to an excessive elongation of the cells, and no multiplication occurred. The movement by which the tips of the leaves and branches are curved toward the base of the stem is caused by internal forces and is not geotropic. Similar reactions were obtained from *Myriophyllum*. *Ranunculus divaricatus* did not exhibit marked change. Excessive elongation of internodes was also shown by *Elodea*.

The effect of light upon bacteria and similar organisms has been the object of several important investigations, a history of which is given briefly by H. M. Ward[97] in the latest paper on the subject. The results obtained by the various workers are by no means in agreement, but it seems fairly well established by Ward that blue, violet and ultra-violet rays exert a fatal effect upon vegetative cells of bacteria and yeasts. These results, however, only have the general significance that the optimum intensity of light for the organisms in question is far below that of direct sunlight.

The results of continuous illumination, as described by Bonnier, are curiously parallel to those of continuous darkness, according to the observations of specimens exposed to the light of electric arcs. Among other features of interest it was noted that the structure of the leaf was more simplified than in the normal, that the epidermal tissues of the petioles were less highly developed, sclerenchymatous elements being lacking, that the structure of the stems was much simpler, and that the customary features of the formation of corky tissue and bark were lacking in a marked degree as well as the differentiation in the parenchymatous tissues. The xylem and pericycle were also less highly developed, in their mechanical features and a special endodermis was formed in *Helleborus niger*. Plants exposed to the electric illumination in question and to darkness in alternating periods of 12 hours showed a fairly normal structure.[98]

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[95] Klemm. Desorganizationserscheinungungen der Zelle. Jahrb. f. wiss. Bot. 28: 627. 1895.

[96] Möbius, M. Ueber einige an Wasserpflanzen beobachtete Reizerscheinungen. Biol. Centralb. 15: 1. 1895.

[97] Ward, H. M. The Action of Light on Bacteria. Proc. Roy. Soc. 185: 961. 1895.

The author of this memoir published a paper dealing with some cultures of seed-plants in darkness and in atmospheres lacking carbon dioxide in 1896.[99] It was proven that material constructed in active chlorophyl-bearing tissues may be transported to inactive organs in darkness and in chambers lacking carbon dioxide in such manner as to permit normal development of etiolated organs in darkness in some species in confirmation of results obtained by Jost. The removal of concurrent organs likewise permitted the full development of organs in some species. The etiolation of a shoot sets in motion regulatory mechanisms by which useless leaves and other organs are cast off in some instances. Later a popular account of etiolations of flowers was published.

F. Darwin[100] called attention to the adaptation theory of etiolation by Godlewsky, in 1896 and pointed out that, lack of light acted as a stimulus and also exerted an effect by disturbing nutrition. The instance of the germination of gemmae of Marchantiaceae only in light was given as in accordance with the theory in question.

Klebs[101] observed the influence of light upon vegetative and reproductive processes of several algae and fungi. The formation of zoöspores appeared to occur most frequently in diffuse light and darkness and conjugation took place in light, the intensity and duration of the illumination being factors in the influence. The blue-violet rays appear to be the cause of the specific action of light in such instances. The formation of zoöspores by *Oedogonium* appears to be entirely independent of light, while on the other hand this process takes place only in light in *Ulothrix*. No generalizations as to retarding effect of light as a direct action may be drawn from these observations.

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[98] Bonnier, G. Influence de la lumière électrique continue sur la forme et la structure des plantes. Rev. Gen. d. Bot. 7: 241, 289, 332, 407. 1895.

[99] MacDougal, D. T. Relation of the Growth of Foliage Leaves and the Chlorophyl Function. Jour. Linn. Soc. 31: 526. 1896.

[100] Darwin, F. Etiolation as a Phenomenon of Adaptation. Jour. Roy. Hort. Soc. 19: 345. 1896.

[101] Klebs, G. Die Bedingungen der Fortpflanzung bei einigen Algen und Pilzen. 1896.

The observations of Stameroff[102] offer some important and accurate evidence upon the influence of light upon the growth of fungi. Vegetative hyphae of *Mucor* and *Saprolegnia* show the same rate of growth in light and in darkness, while light is found to retard the elongation of the sporophores of *Mucor* in corroboration of Vines' experiments upon these organs, but it was not made clear that such retardation was not due partially or wholly to altered transpiratory conditions. Similar retarding action was observed in rhizoids of *Marchantia polymorpha*. The growth of pollen tubes of *Colutea arborescens* and *Robinia pseudacacia* was not affected by light.

Mucor flavidus was seen by Lendner[103] to produce spores only in light; *Mucor racemosus* developed sporangia in darkness but matured spores only in light. Many species of moulds were found to show an excessive elongation of the sporophores in darkness.

Curtel[104] made extensive observations upon the influence of diffuse light upon flowers. He concluded that flowers were less brilliant in color, and fewer in number, and that the peduncles were longer and more slender in diffuse light than in direct illumination. The corolla showed the greatest amount of change, and the stamens and pistils the least. The fruits were smaller and fewer in diffuse light. All of these manifestations might not appear in any one individual. Very diffuse light rendered flower formation impossible and strong diffuse light was quite as favorable as the direct rays. The reactions in question were ascribed to disturbances in nutrition.

Green[105] investigated the effect of light upon enzymes in plants and found that rays located in the red, orange and blue regions caused an increase in the amount of diastase present during the earlier part of the illumination and later acted deleteriously. The violet and ultra-violet rays exerted a constant disintegrating effect. The action of light upon the diastase or enzymes of a cell is, of course, greatly modified by the character of the external membranes, and of the contents of the epidermal cells. The enzymes appear to absorb some of the radiations, but no conclusion is reached as to the fate of the energy transformed.

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[102] Stameroff, K. Zur Frage über den Einfluss des Lichtes auf das Wachstum der Pflanzen. Flora, **83**: 135. 1897.

[103] Lendner, A. Des influences combinèes de la lumière et du substratum sur le dèvéloppement des champignons. Ann. Sc. Nat. VIII. **3**: 60. 1867.

[104] Curtel, M. Y. Recherches physiologiques sur la fleur. Ann. Sc. Nat. VIII. **6**: 220. 1897.

[105] Green, J. R. Action of Light on Diastase, and its Biological Significance. Proc. Roy. Soc. **188**: 167. 1897.

Grantz[106] reinvestigated the relations of fungi to light in 1898. *Pilobolus* formed sterile sporophores in darkness, and the same reaction in other fungi is cited. Etiolated sporophores of *Pilobolus* might produce spores if given only fifteen minutes' exposure to light. Grantz suggests that the etiolation phenomena of fungi are, in fact, reactions to the specific stimulations of light or darkness, and that various correlations are exhibited in these reactions.

A practical confirmation of the conclusions of Jost, MacDougal and others as to the ability of leaves to develop in darkness was made by Vogt,[107] who found that this might occur when these organs were relieved of competition with concurrent members. Similar behavior in atmospheres lacking carbon dioxide was observed, although the duration of the leaf under the latter condition was very limited. Illumination of etiolated seedlings was followed by the attainment of larger size than normal seedlings of the same age.

A general repetition of etiolation tests by Teodoresco,[108] in which entire plants were deprived of illumination, and in other instances branches were thrust into dark chambers gave some interesting results. Leaves borne on such branches always attained a greater size than those on entirely etiolated specimens. The number of stomata per unit of surface was smaller, however. The normal wavy outlines of epidermal cells in leaves unsually lacking in wholly etiolated plants were present to some degree in these etiolated branches, in which also the mechanical properties of the tissues were more nearly normal than in entire etiolations, in lignification and thickening of the walls. *Solanum tuberosum*, *Atriplex hortensis*, *Faba vulgaris*, *Helianthus tuberosus*, *Humulus Lupulus*, *Phaseolus multiflorus*, *Cucurbita Pepo*, *Chenopodium album*, *Aster patulus*, *Cannabis sativa*, and *Saponaria officinalis* were used in these

[106] Grantz, T. Ueber den Einfluss des Lichtes auf die Entwickelung einiger Pilze. 1898.

[107] Vogt, C. Ueber Abhängigkeit des Laubblattes von seiner Assimilationsthätigkeit. Inaug. Diss. Erlangen. 1898.

[108] Teodoresco, E. C. Action indirecte de la lumière sur la tige et les feuilles. Rev. Gen. d. Bot. **11**: 369, 430. 1899.

Teodoresco, E. C. Influence des différentes radiations lumineuses sur la form et la structure des plantes. Ann. Sc. Nat. Bot. VIII. **10**: 141–164. 1899.

tests. The general subject was treated more fully in an extended paper in the same year in which the following additional points are made: Etiolated plants have the outer walls of the epidermis without the papillose convexities characteristic of other individuals of the same species grown in light. Intercellular spaces are lacking in mesophyl of etiolated leaves, and is composed of isodiametric cells. The palisade cells show some differentiation. Stomata were observed by Teodoresco to be more numerous in a given area than in normal specimens, and also to be smaller. The notable lack of differentiation of tissues in etiolated plants was observed and attention was called to the lack of formation of the generative layers, and of secondary tissues. Similar lack of development of xylem and of bast fibers was noticed.

The multiplication of observations upon fungi in which light is found to exert no influence is a notable feature of the most recent investigations. Klebs[109] joined in such results and found that growth of the vegetative organs as well as the reproduction of many forms was utterly uninfluenced by the radiations. Furthermore the growth of sporophores in many species occurred absolutely indifferently in light and darkness. The single instance of retardation of growth of the sporophore of *Phycomyces* and *Mucor* by Vines and Stameroff does not have the concurrence of Bullot,[110] who affirms that these organs grow more rapidly in continuous light than in darkness. Light has been found necessary for spore formation except in the single example cited by Klein. In such observations the critical points are well defined and the intensity of illumination may be increased to a point where an unfavorable action is exerted, and the phototropic behavior reversed. Klebs has pointed out the necessity for the strictest control of experimental tests of fungi in light since the separate results of altered transpiration and nutrition may mask or alter the effects of the illumination. These results are confirmed in the main by Ternetz,[111] and other investigators quoted by Klebs and Ternetz.

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[109] Klebs, G. Zur Physiologie der Fortpflanzung einiger Pilze. Jahrb. f. Wiss. Bot. **35**: 140. 1900.

[110] Bullot, E. Sur la croissance et les courbes du Phycomyces. Ann. d. l. Soc. Microscopique d. Belge, **21**: 84. 1897.

[111] Ternetz, C. Protoplasmabewegungung Fruchtkörperbildung bei *Ascophanes carneus* Pers. Jahrb. f. Wiss. Bot. **35**: 273. 1900.

Brenner[112] attributed the abnormal forms of succulent species of seed plants in darkness to disturbances of transpiratory conditions on one hand, in addition to an adaptive elongation of the shoot for the purpose of reaching the light.

The investigations of Thomas[113] in which instructive comparisons were made between the characters of subterranean and aërial leaves are of great interest. Leaves normally or experimentally developed as underground scales cutinize both upper and lower surfaces, and diminish the formation of collenchyma, palisade cells and intercellular spaces. Decrease in vascular tissues, disappearance of projections and irregularities of contour, diminished development of sieve tubes and stereome are also features of such growth, and are parallel to those shown in etiolation. Underground leaves may also lose the stomata when used for storage.

Maige[114] brought out some interesting observations on the geotropic reactions of creeping plants in darkness. Two groups are distinguished according to their reaction in darkness. One group, including *Hieracium pilosella* and *Mentha sativa*, places its branches in an erect position in darkness, and a second, of which *Potentilla reptans* is representative, does not.

Stigeoclonium tenue has been found to remain green and healthy in darkness for periods of three to five weeks, and such deprivation of illumination did not alter the response to the osmotic and nutritive influence of solutions, according to the observations of Livingston,[115] an endurance which is of interest in connection with the determination of the term through which chlorophyl may be maintained in darkness.

Goff[116] relates that the first node of seedlings of corn usually is to be found near the surface of the soil, regardless of the depth at which the seeds may be planted. Seedlings in darkness showed such elongation of the first internode that the node was raised some distance above the soil.

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[112] Brenner, W. Untersuchungen an einigen Fettpflanzen. Flora, 87: 387. 1900.

[113] Thomas, J. Anatomie comparée et expérimentale des feuilles souterrainnes. Rev. Gen. d. Bot. 12: 394. 1900.

[114] Maige, A. Recherches biologiques sur les plantes rampantes. Ann. Sc. Nat. VIII. 11: 345. 1900.

[115] Livingston, B. E. Further Notes on the Physiology of Polymorphism of Green Algae. Bot. Gazette, 32: 298. 1901.

[116] Goff, E. S. Influence of Light on the Length of the Hypocotyls in Indian Corn. Science, 13: 395. 1901.

Ricome[117] has made a series of examinations of the behavior of etiolated plants placed in light before deterioration of the shoot had begun and his chief results are as follows: The excessive growth in length of stems slackens quickly when etiolated plants are illuminated and the rate of growth remains slower than that of control specimens. If, however, abundant reserve material is at hand the rate is not sensibly slower than the normal, except at the beginning of the illumination. Mature shoots of illuminated etiolated specimens are longer than normal if such reserve material is present, but shorter otherwise. The internodes at the base of the hypocotyledonary axis are more slender than the normal in such plants unless ample reserve material is present. The basal internodes formed in darkness are elongated in light but the internodes formed immediately after exposure seem to be shorter than the normal, or those formed later above them, which have the normal length. This seems to be due to the disturbances in the transpiratory conditions. The number of leaves of illuminated etiolated specimens is less than in normal specimens. Etiolated plants without reserve food do not attain the normal weight when illuminated, although this is accomplished by plants with a reserve food-supply. Illuminated etiolated plants have a comparatively greater dry weight than normal specimens. If plants with reserve food are etiolated for a short period and then illuminated they will appear more vigorous than normal specimens for some time, a result that has been confined by Dr. H. M. Richards in some experiments in his own laboratory.

Noll[118] concludes that darkness as such acts as a positive stimulus in producing etiolation phenomena and finds that similar reactions may be obtained from other causes, such as in the growth of roots in solutions lacking nitrogen. Phenomena resembling etiolation have been induced in algae by Benecke[119] by the use of culture solutions lacking nitrogen.

Wiesner[120] likewise was able to secure excessive elongations of stems by cultivation of plants in chambers of low humidity, externally resembling those resulting from etiolation. No anatomical comparisons were made, however.

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[117] Ricome, M. H. Sur le développement des plantes étiolées ayant reverdi à la lumière. Compt. Rend. 131: 1251. 1900.

Ricome, M. H. Action de la lumière sur les plantes préablement étiolées. Rev. Gen. d. Bot. 14: 26, 72, 120. 1902.

[118] Noll, F. Ueber das Etiolement der Pflanzen. Sitzungsber. d. niederrheim Ges. z. Bonn. May, 1901. Abstract, Botan. Ztg. 60: 38. 1902.

[119] Benecke, W. Ueber Cultur Bedungungen einiger Algen. Bot. Ztg. 56: 1st Abth. 89. 1898.

[120] Wiesner, J. Formänderungen von Pflanzen bei Cultur im absolut feuchten Räume. und im Dunkeln. Ber. d. Deut. Bot. Ges. 9: 46. 1891.

By the recent researches of Nabowick[121] etiolated seedlings of maize, sunflower and onion were found capable of anaërobic growth, although further evidence upon the matter is needed.

Neljubow[122] describes the horizontal positions assumed by stems of *Pisum* and other plants in darkness and ascribes these positions to the influence of various external forces, the relations of which are not made clear.

Undoubted instances of growth which is accelerated or facilitated by light are given by Schulz[123] as the result of observations on spores of mosses, ferns and equisetums. Germination of these bodies are said to occur only in light with the exception of those of *Ceratopteris thalictroides* and the Ophioglossaceae. In some instances the stimulating action of the rays is necessary to start growth, while in others, growth must wait on the construction of material by the chorophyl apparatus before new cells of protoplasm may be built up. It was found possible to replace the stimulating influence of light by that of other forces in a few instances.

These results are in accord with those attained by Borodin[124] thirty-four years earlier. Borodin tested the spores of *Aspidium spinulosum foenisecci*, *Ancimia Phyllitides longifolia*, *Allosorus sagittatus*, *Aspidium molle*, *Polypodium repens*, *Phegopteris effusa*, *Asplenium alatum*, *Asplenium lasiopteris* and another species of *Asplenium* and found that light was an indispensable condition of germination of these forms, the least refrangible rays being active in the matter, the blue rays having the same effect as darkness. Milde[125] had previously reported that spores of *Equisetum* would germinate in darkness although this result has not been confirmed.

No attempt has been made in the foregoing sketch to review the literature of influence of light upon germination of seeds. It is well

[121] Nabowick, A. Wie die Fähigkeit der Höheren Pflanzen zum anaeroben Wachstum zu beweisen und zu demonstriren ist. Ber. d. deut. Bot. Ges. **19**: 222. 1901.

[122] Neljubow, D. Ueber die horizontale nutation der Stengel von *Pisum sativum* und einiger anderen Pflanzen. Beih. Bot. Centralb. **10**: 128. 1901.

[123] Schulz, N. Ueber die Einwirkung des Lichtes auf die Keimungsfähigkeit der Sporen der Moose, Farne, und Schachtelhalme. Beih. Bot. Centralb. **11**: 81. 1901.

[124] Borodin, J. Ueber die Wirkung des Lichtes auf einige höhere Kryptogamen. Mel. Biol. **6**: 529. 1867.

[125] Milde. Zur Entwickelungsgeschichte der Equiseten und Rhizocarpen. Nova Acta Acad. L. C. **23**: 2.

known that illumination is indispensable to germination of some species, and that darkness is equally necessary for others. In both instances the stimulating effect is probably concerned, although the action of the heat rays is not eliminated.

The foregoing résumé may be held to include notices of nearly all of the more important researches bearing upon the subject of this paper. Doubtless some worthy of notice have escaped the author's attention, and still a few others will be referred to in the discussion in the closing section of this memoir.

SCOPE, PURPOSE AND METHODS OF THE PRESENT OBSERVATIONS.

In the earlier investigations of the author[126] upon the growth of plants in darkness, and in atmospheres lacking carbon dioxide, conclusions of value concerning the relation of development to nutrition, and as to the regulatory action of the plant in darkness were reached. It was found, however, that a satisfactory explanation of the phenomena of etiolation might not be made from any such limited series of experiments, and that current generalizations as to the relation of light to growth and reactions of plants in darkness rested upon similarly isolated series of observations in which only a few species of plants were used, and under conditions not always under full control. It was therefore planned to carry out a large number of etiolations upon species selected to represent types of the most diverse morphological and physiological character and habit. In the seven years during which the work has been in progress ninety-seven species have been cultivated in continuous darkness with control plants in ordinary alternation of daylight and night. Aquatics, creepers, climbers, succulents, mycorhizal forms, geophilous and aërial shoots, mesophytes and spiny xerophytes, were grown from tubers, corms, rhizomes, cuttings of leaves and stems, seeds and spores.

By the extension of the observations over such an extended period, it was also possible to obtain much interesting and valuable information as to the inertia, or capacity for endurance of species with storage organs under conditions not suitable for the acquisition of formation of complex organic food, a subject hitherto but little touched.

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[126] MacDougal. Relation of Growth of Leaves to the Chlorophyl Function. Jour. Linn. Soc. London, 1: 526. 1896.

The earlier etiolations from 1895 to 1899 were made at the University of Minnesota in small portable chambers of zinc and wood, and the cultures were examined for a few minutes every day in daylight, a method which is found to offer results markedly different from those kept in absolute darkness and examined by the light of a single candle not oftener than once a day.

For a portable chamber the best material was found to be zinc, and this was built in the form of a small house with no bottom. The entire chamber rested upon a bed of sand about 5 cm. in depth, upon which the plants were placed. The chamber was lifted from its position by means of a cord attached to the top passing over a pulley fastened to a beam above. When the chamber was lowered to its position the edges were imbedded in sand in such a manner as to exclude light absolutely. Ventilation was provided by means of tubular openings to which sections of rubber tubing were attached. The curvatures of the tubing prevented access of light. Such portable chambers were protected from the direct action of the sun's rays, and injurious temperatures were thus avoided.

Upon my removal to the New York Botanical Garden in 1899 the work was resumed in a specially constructed dark chamber. This chamber measures 5 x 5 x 6 meters and is situated in the middle of the laboratory suite on the fourth floor of the museum building, and is provided with ample connections with ventilating shafts in such manner that the atmosphere is always normal. Cultures were made here between October and May of each year, and during this period the temperature was constant between 17 and 21° C., and did not traverse this range in less than four days, so that for most purposes a constant temperature was provided in these tests. It is to be understood of course that this temperature is by no means suitable for all of the forms upon which observations were made, a fact which was duly noted in the descriptions of the separate experiments; it did permit, however, a fairly etiolated normal development of almost all of the species examined. Entrance to the chamber was gained by a set of double doors with a vestibule between in such manner that no daylight was admitted. Examination of the plants was made by means of the light afforded by a single candle, or an electric hand-lamp of four candle-power.

In a few instances the etiolated specimens were removed for the purpose of making photographic negatives, but generally this was not done until the completion of the experiment. Control specimens were cultivated in the physiological laboratory on the same floor of the building, or in the experiment chamber of the propagating houses.

The illustrations are mainly drawings from photographic prints, from natural objects and from microscopic sections, and were made by Miss Alexandrina Taylor, and Mr. Auguste Mariolle.

The details of the observations on the several species of plants brought under examination are given on the following pages.

Agave Americana L.

Specimens with thick fleshy leaves 25 to 40 cm. in length were placed in the dark chamber in September, 1900, and the observations were closed in May, 1901. Leaves which had not reached maturity at the beginning of the test elongated by basipetal growth, forming a pale yellow etiolated basal portion. The chlorophyl in the older green portion was maintained in an apparently normal green condition during the entire eight months. Leaves emerging after the beginning of confinement attained only half the length and thickness of the normal, and were capable of extended existence in the dark room. This endurance is coupled with the fact that the stomata were present in the etiolated epidermis, open and apparently normal in form with the guard cells richly loaded with starch.[127]

The leaves were not so rigid as the normal. The teeth along the margins were present, but were not so prominent as in the green specimens. The outer walls were slightly cutinized, less so than the normal, and did not show the usual thickening. The development of the fibrovascular bundles was apparently arrested in an early stage of the differentiation of the phloëm and xylem. Spiral vessels were fully formed, however, and could be pulled out in the usual manner.

No indications of flower spikes were to be seen in the etiolated plants, or in the control tests.

Allium Neapolitanum Cyr.

Bulbs of *Allium Neapolitanum* were placed in the dark chamber in March, 1901 and soon began to send out leaves. The bases of the leaves were sheathing and adherent to a distance of about 5 cm. from the bulb in both the normal and etiolated examples. Normal leaves were about 2 to 2.5 cm. in width are about 20 cm. long, being curved and twisted. Etiolated leaves attained a length about equal to the normal with inrolled margins and with a width of 12 to 15 mm. The curvatures and torsions were much more marked than in the normal, and the positions assumed were indicative of an entire lack of geotropic sensibility. It is to be noted that this plant offers an example of a monocotyledonous leaf which does not exceed any of the dimensions of the normal. A creamy yellow color points to the presence of a large amount of etiolin or carotin.

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[127] Thomas, J. Anatomie comparée et experimentale des feuilles souterrainnes. Rev. Gen. d. Bot. **12**: 394. 1900.

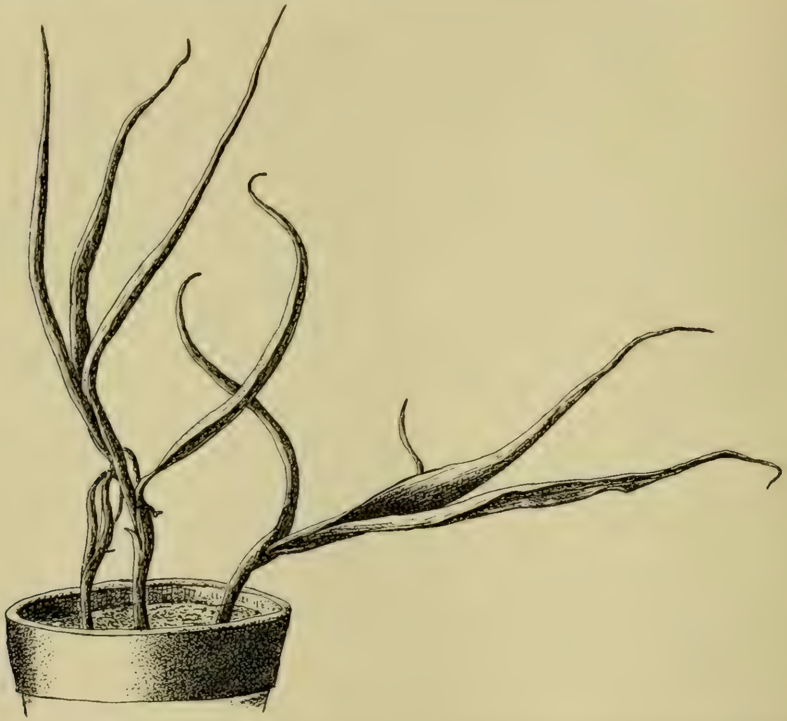

FIG. 1. *Allium Neapolitanum*, etiolated, showing positions and forms assumed by leaves. ⅓ natural size.

Sachs[128] records that *Allium Cepa* developed etiolated leaves longer than the normal and variously divergent. Such leaves were thinner than the normal and were lacking the central lysigenous cavity, as were also those of *A. Neapolitanum.*

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[128] Sachs. Ueber den Einfluss des Tageslichtes auf Neubildung und Entfaltung verschiedener Pflanzenorgane. Ges. Abhandl. 1: 196. 1892. See also Sachs. Handbuch der physiologischen Botanik, p. 38. 1865.

The inflorescence axis showed no sign of activity and was wholly undeveloped in all examples dissected. After a growth of the leaves had been made in darkness, the outer scales from which they have been nourished were spent and empty. The scales composing the central core were solid and turgid forming an ovoid mass about 12 mm. in cross section. It is probable that these scales would have furnished material for the growth of the inflorescence in normal growth. Sachs speaks of the formation of seeds by *Allium porrium*, which presumably had more or less nearly reached maturity before confinement in the dark chamber.

Allium vineale L.

Bulbs of *A. vineale* were brought into the dark chamber from the open air in April, 1900, and the leaves showed a rapid growth, soon reaching an ultimate size which was slightly less in length than in the normal. In a few instances the average measurement was reached, however. The width was less than in the normal. In contrast to *A. Cepa* and *A. Neapolitanum* the lysigenous splitting of the internal parenchyma was observed to take place in the usual manner.

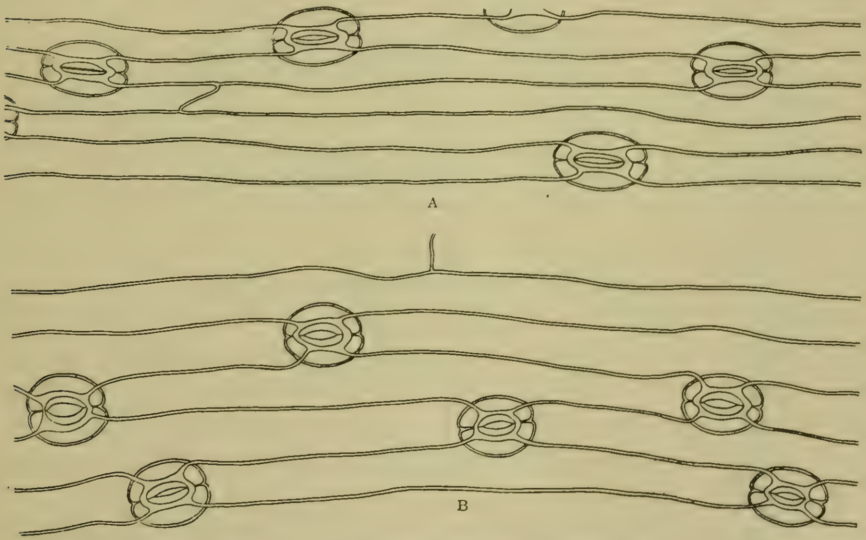

FIG. 2. *Allium vineale.* *A*, etiolated epidermal cells of leaf. *B*, normal epidermal cells of leaf. × 100.

The epidermal cells were much longer and narrower than in the normal, which was also true of the guard cells of the stomata. The latter showed a narrow slit, and were slightly functional. The existence of the leaves covered only a few weeks. The exaggerated length of the epidermal cells in this species is seen not to be accompanied by a corresponding increase in the measurement of the length of the leaf, hence the number of epidermal cells developed must be smaller than in the normal. The inflorescence axis failed of development entirely.

Amaryllis Johnsoni Bury.

Awakening bulbs of *Amaryllis Johnsonii* placed in the dark chamber in April, 1901, showed a fairly normal elongation of the scape. The flowers opened in the usual manner with the pistil extruded to a length of 2 cm. beyond the stamens. It is to be noted that the unopened flower bud in this instance was subject to the action of light for some time before growth began, and that ample opportunity was afforded for the exercise of a stimulating effect.

Amorphophallus Rivieri Dur.

A large corm of *Amorphophallus Rivieri* was placed in the dark room in a resting condition in March, 1900. The soil was allowed to become slightly drier than that necessary for germination until September, 1900, when water was applied daily. The flower bud opened in October and the scape began to elongate at a rate which increased until it amounted to 20 cm. one day and 25 cm. on another, after which the rate decreased to minimum. A total length of 1.8 meters was reached within three weeks. The three sheathing scales at the base of the scape were 12, 22 and 35 cm. in length, which is much greater than that of the normal. The attainment of full length of the scape was marked by the appearance of the roots from the upper internode of the corm, these organs being entirely dormant until this time.

The development of the scape and flower was accompanied by a striking display of color. The scape was slightly fluted, pale red in color with mottled patches of violet, and exuded sap freely when cut across. The spathe was only slightly flaring at the top where it was a deep rose purple, shading lighter to the base, where it was a pale rose tint. The spathe reached a length of 40 cm. and the inner surface of the lower portion was deeply rugose and purple for a distance of

10 cm. from the base. The pistillate flowers occupied a zone about 8 cm. long on the spadix, and were flaccid and pale rose color. The staminate flowers occupied a zone 7 cm. wide above them, and were of a brownish hue. Both stamens and pistils did not reach normal development and were not capable of carrying out seed-formation. The irregular club-shaped end of the spadix was hollow by reason of the central cavity of lysigenous origin. The portion of the spadix above the flowers was 50 cm. in length and became curved at maturity while still turgid and firm. The spathe was seen to be furnished with many stomata, which were open when examined in water, and the guard cells of which were richly loaded with starch. Similarly developed and active stomata were found on the epidermis of the scape. The characteristic unpleasant odor of the plant was noticeable, but not so strongly as in examples grown in light.

The scape and the flower endured for a period of about five weeks from the beginning of growth and then quickly perished. Immediately a swelling bud at one side of the base of the scape began to increase in size very slowly. The corm was allowed to go into a resting stage in May, 1901, and again watered and given favorable cultural conditions in September, 1901, but the slow increase of the bud ceased and no leaf had been developed as late as May 27, 1902. This bud occupied the position of the leaf, which ordinarily begins growth after the maturity of the flower, and contemporaneously with the growth of the roots. The growth of the roots in an etiolated specimen continued more or less freely during the entire period after their first appearance. The corm was taken from the soil on the last named date, and in addition to a great number of rudimentary buds

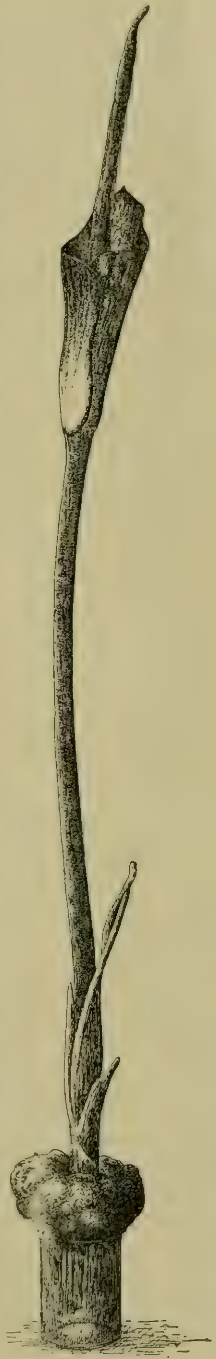

FIG. 3. Etiolated scape of *Amorphophallus Rivieri*. Aspect of plant, including corm, upon maturity of scape and before curvature of end of the spadix had begun.

and roots had formed two large branches of a corm-like structure. The apices of these branches were crowned with long buds curved apogeotropically, and containing a young leaf. The failure of the scape to reach light from the opposite, upper surface, may have stimulated the formation of these leaf buds from the lower side.

The scape shows an exaggerated elongation, in conformity with the fact that it must find its way up to the light unaided under all circumstances. The soundness of the corm after the first growth in darkness suggests that it might be capable of long-continued existence without light after a manner more fully described in the discussion of *Arisaema*.

Apios Apios (L.) MacM.

Tuberous stems of *Apios* were placed in the dark chamber on February 14, 1900. These specimens had remained in the soil in the open during the preceding winter months and the shock of the

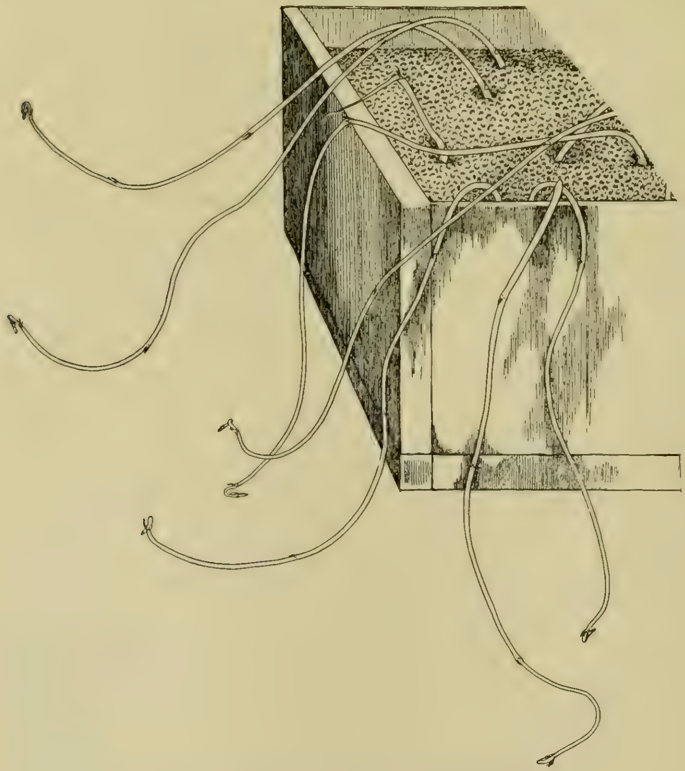

FIG. 4. Etiolated stems of *Apios Apios*.

change in temperature soon awakened the buds and the formation of stems was carried on vigorously. March 19, stems 10 to 30 cm. long were to be seen. The stems were decumbent and trailing with the apices directed upward in accordance with their apogeotropism. Repeated tests were made by placing the terminal portions of the stems in contact with supports but in no instance were any manifestations of twining to be observed. March 28, stems 30 to 45 cm. were measured and the internodes in the terminal half were found to have a greater diameter than those of the basal portion. The comparative lengths of the internodes are shown by the following figures:

ETIOLATED.

Basal,	6	8.5	9	6.5	9	7	6	6	4	5	4	Apical.
Basal,	9	7	10	9.5	8.5	6	6.5	6	6.5	5		Apical.

NORMAL.

Basal,	4	9	9	8		Apical.
Basal,	4	10	13	9	8	Apical.

It is to be seen that the basal internodes attained greater length in the etiolated specimens, but that the maximum length of the etiolated internode was not greater than in the normal. The number of internodes was greater in etiolated examples than in normal of the same age, but the ultimate number developed in the normal was greater of course. The shorter internodes in the terminal portion of the stems were still in process of elongation in both etiolated and normal examples at the time the above measurements were made.

The etiolated stems were free from trichomes, which were very abundant on normal green stems. The stipules were nearly normal in size and form, but the remainder of the leaf was represented by a short petiole 1 to 2 mm. long bearing three rudimentary leaflets the laminae of which were not more than 1 mm. in length. The axillary buds were of about the same length as the petioles, and those near the apex might easily be started into activity by the destruction of the terminal bud.

Marked divergences from the normal were to be found in the internal anatomical characters of the stem. The epidermal cells were more than twice the length of the normal and were also much wider in surface view. The increase in width was exactly correlated with the increased thickness of the etiolated stem, but the relation of the increased length was not clear, unless perhaps it might be said that the normal cells had not attained full growth. The cortical cells were larger in the etiolated stems and presented quite a different aspect, being arranged with their longer diameters radial, while in the normal the greater diameter is tangential. The number of layers of these cells was greater, and the individual elements showed a more rounded contour, with large intercellular spaces. The normal cortex has but sparing intercellular spaces, and the outline of the cells in transverse section shows well-defined angles.

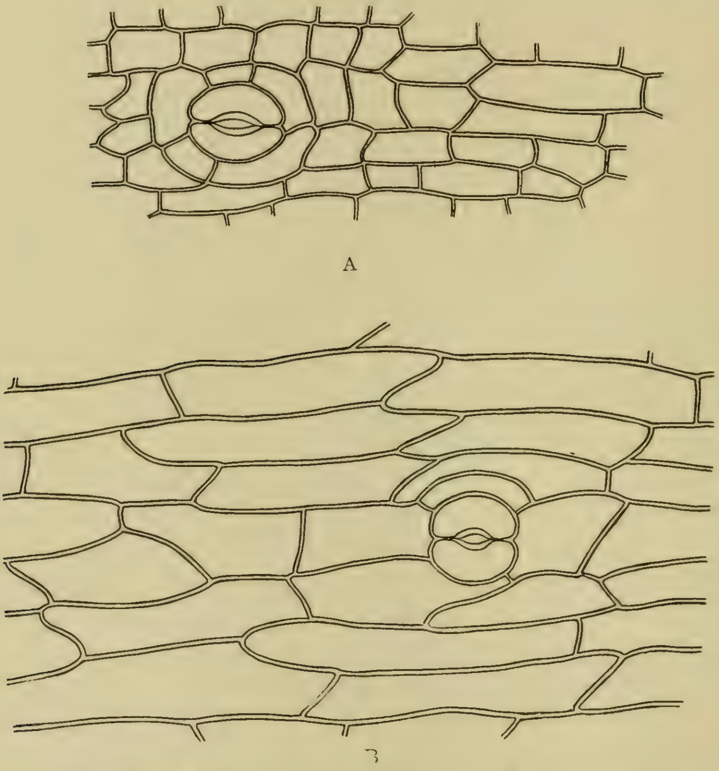

FIG. 5. Surface view of epidermal cells of stems of *Apios Apios: A*, normal; *B*, etiolated. × 250.

But little difference could be found between the xylem of the normal and etiolated stems. External to this however the changes were most marked. The etiolated stem developed a distinct and continuous cambium with many layers and the sieve tissue was not to be made out with certainty, as in the normal. The space between the cambium and the bast fibers was occupied by a mass of elongated parenchymatous cells with large lumina. The bast fibers were to be made out but were very sparingly thickened. Externally to the bast was a tract of two to five layers of cambiform cells which seemed to be very active. The formation of this secondary generative region is certainly a remarkable occurrence, and is one which finds a parallel only in *Castanea*, *Hicoria* and *Quercus* among the species examined (see Fig. 7, *C*).

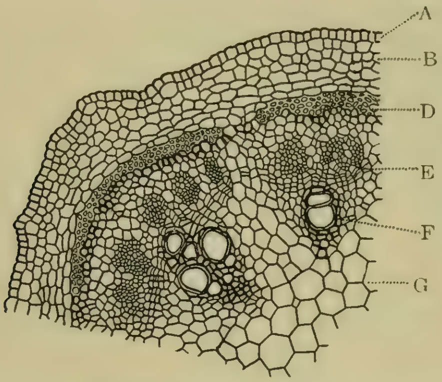

FIG. 6. *Apios Apios.* Transverse section of portion of aërial normal stem; *A*, epidermis; *B*, cortex; *D*, bast fibers; *E*, cambium; *F*, xylem; *G*, pith. ×40.

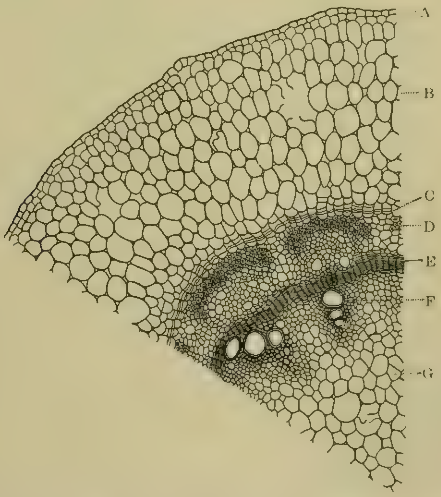

FIG. 7. *Apios Apios.* Transverse section of portion of etiolated stem; *A*, epidermis; *B*, cortex; *C*, generative layer; *D*, bast fibers; *E*, cambium; *F*, xylem; *G*, pith. ×40.

Nearly all of the tubers from which etiolated stems were developed in these cultures survived and contained a large amount of storage material, and some of them showed a second growth similar to the first, without perishing. *Apios* may be classed as a plant capable of making more than one effort in different seasons to carry leafy stems up to sunlight.

Aplectrum spicatum (Walt.) B.S.P.

Fourteen vigorous specimens of *Aplectrum spicatum* were placed in the dark chamber on December 27, 1898, and soon awakened. Leaves were formed which reached maturity in May, 1899. Similar cultures were also made in the following year. These leaves were formed at the extremities of offsets which run 2 or 3 cm. laterally from an old corm and then develop the terminal internodes as a corm with its apical bud apogeotropic. The leaves are put out during the season of swelling of the corm. The young corm receives storage matter both from the old corm and from the active new leaf. In the etiolated specimens the corms thus formed attained about twice the length of the normal, with the longitudinal diameter much greater than the transverse, which is the reverse of the normal behavior.

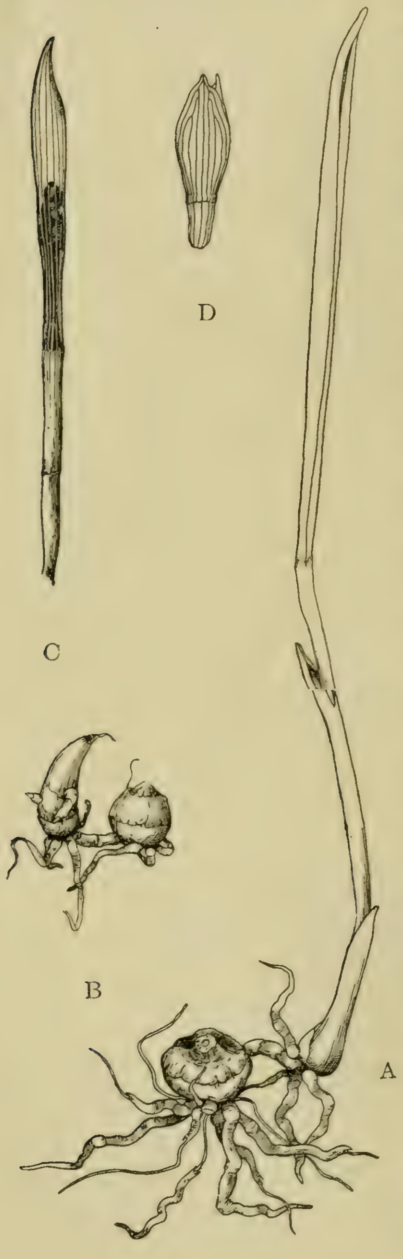

FIG. 8. *Aplectrum spicatum*. *A*, etiolated plant with young corm, scales and attenuated leaf. *B*, old corm and young corm formed in darkness. *C*, inflorescence of etiolated plant. *D*, single etiolated flower.

The outer and lowest sheathing scale attained a length of 3 cm., and the scale from the median node of the new corm was 9 cm. long, while the leaf arising from the upper end of the terminal node attained a length of 25 cm., which is about double that of the normal. The excessive development is distributed throughout the entire length of the leaf, so far as my examinations may be depended upon. The upper portion remained folded plicately in a cylindrical mass a few millimeters in diameter, and the total width when artificially extended was not more than one-fourth of the normal. Numerous stomata were formed which were open when examined in alcohol.

About the time that the leaves reached maturity, offsets from the young corm were sent off, which in some instances had the coralloid form taken in certain mycorhizal adaptations which I have previously described.[129]

The development of the leaves usually occurs at the close of a vegetative season, and these organs live through the winter, falling away in the spring, when the scape arises axially to the leaf scars. In the etiolated examples, however, the development of the leaves covered a period from December 27 to May following, and the inflorescences began to push up in March before the growth of the leaves was completed. The flowering branch is composed of two or three internodes. From the upper end of the uppermost internode a scale 8 to 15 cm. long arises completely sheathing the flower bud, its edges being fused to form a complete covering. An inner scale with a length of 6 cm. also sheathes the flowers in the same manner. These two scales remain intact and the flowers perish without being exposed to the air. The separate pedicels attain a length about a half greater than the normal, and the floral envelope in the separate flowers is much reduced, although the pollinia appear fairly normal in stature. A third outer sheathing scale inclosing the inflorescence is pushed open by the flower bud with its double coat.

Etiolated corms made a second growth in the dark chamber after a resting period of four months. The second series of etiolated leaves were smaller than the first. No flower buds were formed. Many of the corms were seen to be alive after the second growth in the dark, but no further action could be secured from them.

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[129] MacDougal. Symbiotic Saprophytism. Annals of Botany, 13 : 1. 1899.

Arisaema Dracontium (L.) Schott.

Corms of *Arisaema Dracontium* were placed in the dark chamber in 1897, 1898 and 1899. After a proper resting period had been given, the terminal buds would begin to enlarge about five weeks later, and roots were sent out from the upper internode which penetrated the soil in all directions. These roots as well as those of *Amorphophallus* and other aroids often emerged into the air, and were only directed back into the soil after a length of a centimeter or two had been exposed, as if the sole directive force were moisture.

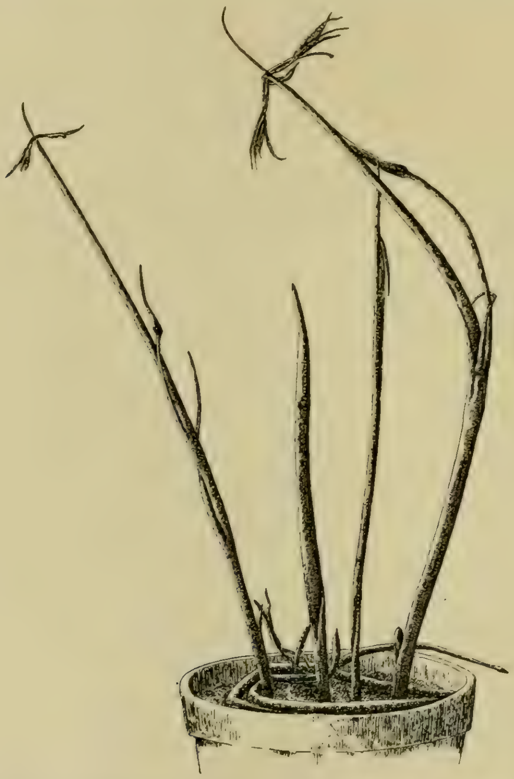

FIG. 9. Culture of etiolated plants of *Arisaema Dracontium*, showing several stages of development of the buds, scapes and flowers.

After about five weeks from the beginning of the culture the buds reached a length of 25 to 30 cm., at which stage the prophyll, which had hitherto completely enclosed the leaves and flower, would split and an elbow or curved portion of the petioles of one of the leaves would be thrust out. After a time the leaves and flowers would become entirely freed from the bud. The leaflets remained tightly folded together and were of a rich yellow color. The spathe remained tightly wrapped around the spadix, was smaller than the normal and also of a pale yellow color. The scape did not attain a length comparative to that of the petioles. Normally the attenuated tip of the spadix is thrust out above the leaflets, but in these etiolated examples it remained much shorter. The etiolated spadices were about normal length. The stamens and pistils did not reach normal stature, and attempts at pollination met with no result as to seed formation.

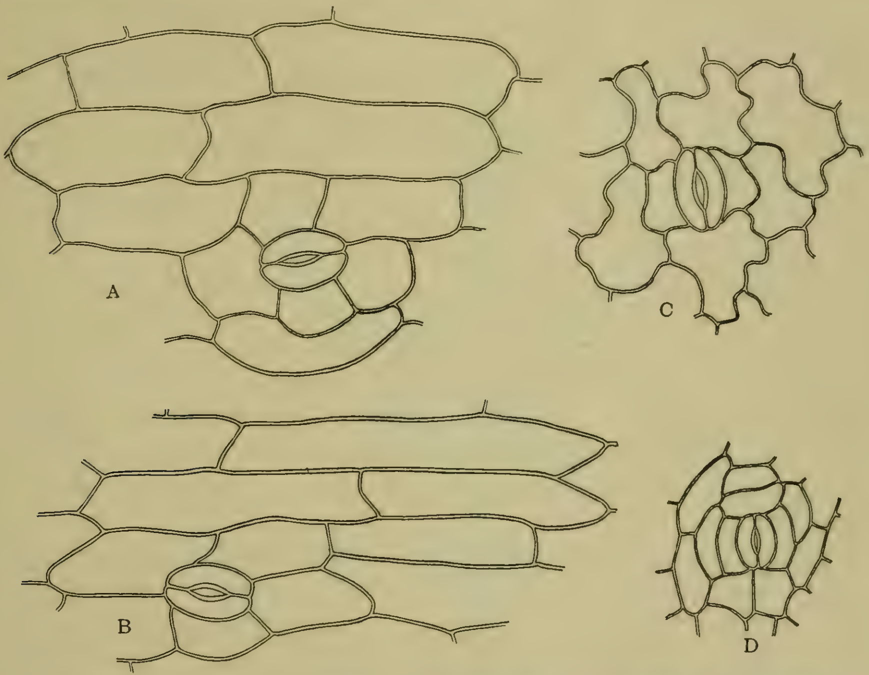

FIG. 10. *Arisaema Dracontium.* *A*, epidermis of normal scape. *B*, epidermis of etiolated scape. *C*, epidermis from lower surface of normal leaflet. *D*, epidermis from lower surface of etiolated leaflet. × 190

The scapes and scape were more slender than the normal. The altered dimensions of the epidermal cells did not correspond to these changes, however. Measurements of a number gave an average length of 38 for the normal and 32 for the etiolated epidermal cells of the scape. The width of normal cells was 10 and of the etiolated 11. Stomata of normal scapes measured 10 by 12 in one series and 10 by 11 in another. Stomata of etiolated scapes measured 8 by 10 and 8 by 11. The stomata were slightly open when examined in water.

Corms surviving the first etiolation were given a period of rest, when they were again set in action, and produced buds of not more than half the length of the first etiolated growth. No flowers were formed in this second etiolation, however. Many of the corms were sound and alive after the second etiolation, and remained quiescent two years and are still dormant at the date of preparation of this memoir (June, 1902).

Attention has been called to the saprophytic etiolated growth of the seedlings of *Arisaema Dracontium* in a previous paper. The germination of the seed results in the formation of a hypocotyledonary stalk which is pushed down into the soil carrying with it the plumule which remains in an undeveloped condition. The base of the hypocotyl soon begins to swell and the surplus food in the seed is withdrawn into the tuber thus formed, which bears the quiescent plumular bud at its apex. The entire season is thus spent underground, and the saprophytic existence of the seedling is much prolonged.[130]

Arisaema triphyllum (L.) Torr.

Arisaema triphyllum lent itself most readily to etiolation experiments and it was used in obtaining data on several general questions in the investigations. Several hundred cultures have been made in the dark chamber, and this plant has been under continuous observation from 1895 to 1902.

Corms placed in the dark chamber after a proper resting period would soon begin to show indications of activity. Ordinarily the terminal bud of the corm elongates to a length of 5 to 7 cm. and then splits, allowing the leaves and flowers to escape. The sheathing bases of the two leaves enclose the base of the scape to a distance of 4 to 8 cm. from the corm, and the petioles attain a length of 15 to 75 cm., which is something longer than the scape. A second scale sheathes the base of the bud and has a length of 2.5 cm. A third basal scale rarely reaches a length of over a centimeter. Marked departures from this procedure were shown by etiolated cultures. The prophyll elongated excessively, attaining a length of 8 to 50 cm. before it splits for the emergence of the leaves and flower. The second scale attained a length of 4 to 7 cm. and the third about half that length. This test was made in another form by placing plants with awakening buds in an exposed situation and covering the buds with a heap of sphagnum to a depth of 30 cm. Similar elongation of the prophyll was made and the bud was not opened

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[130] MacDougal. Seedlings of *Arisaema*. Torreya, **1**: 2. 1901. See also Rennert, R. J. Seeds and Seedlings of *Arisaema triphyllum* and *Arisaema Dracontium*. Bull. Torrey Club, **29**: 37–54. 1902.

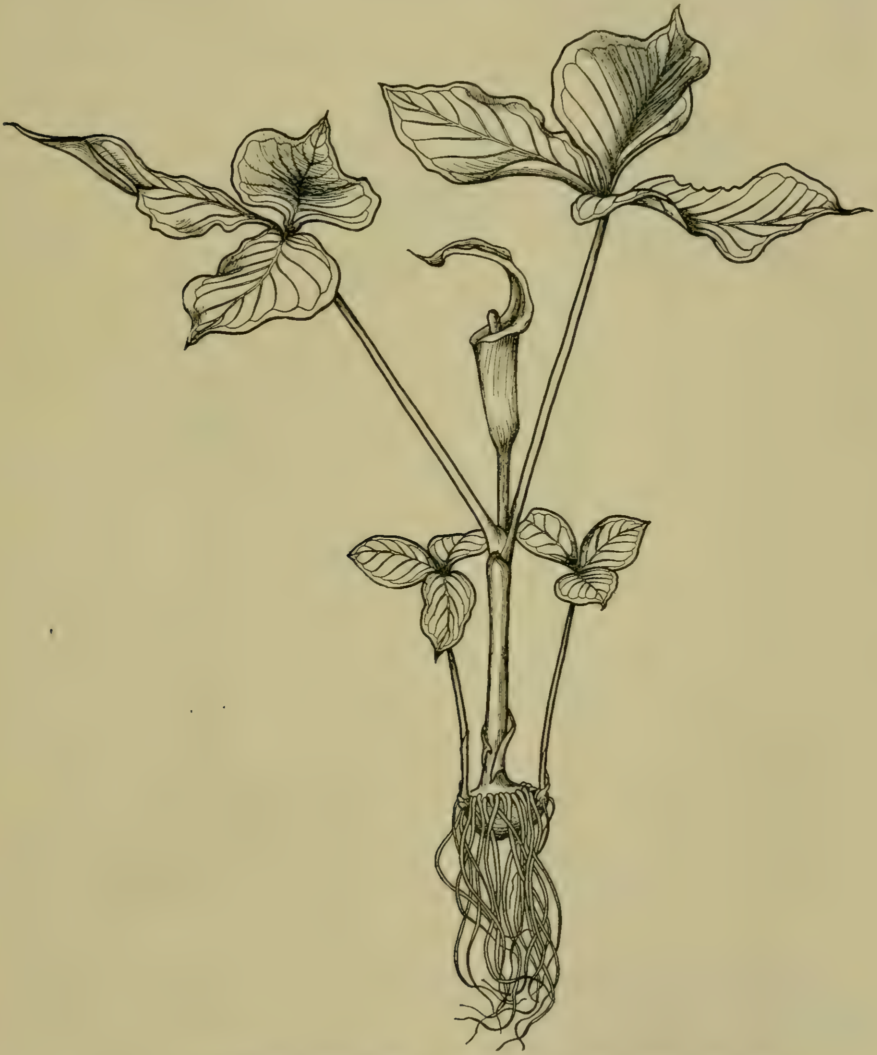

FIG. 11. *Arisaema triphyllum.* Normal, with two latera plantlets.

till the tip of the prophyll had been stimulated by light. Still a third experiment was made to determine the capacity of the plant for piercing obstacles between its bud and light; a number of corms were buried to a depth of 25 cm. in loose garden loam and the prophyll reached the surface of this substratum before opening. The mechanical force exerted must have been very great.

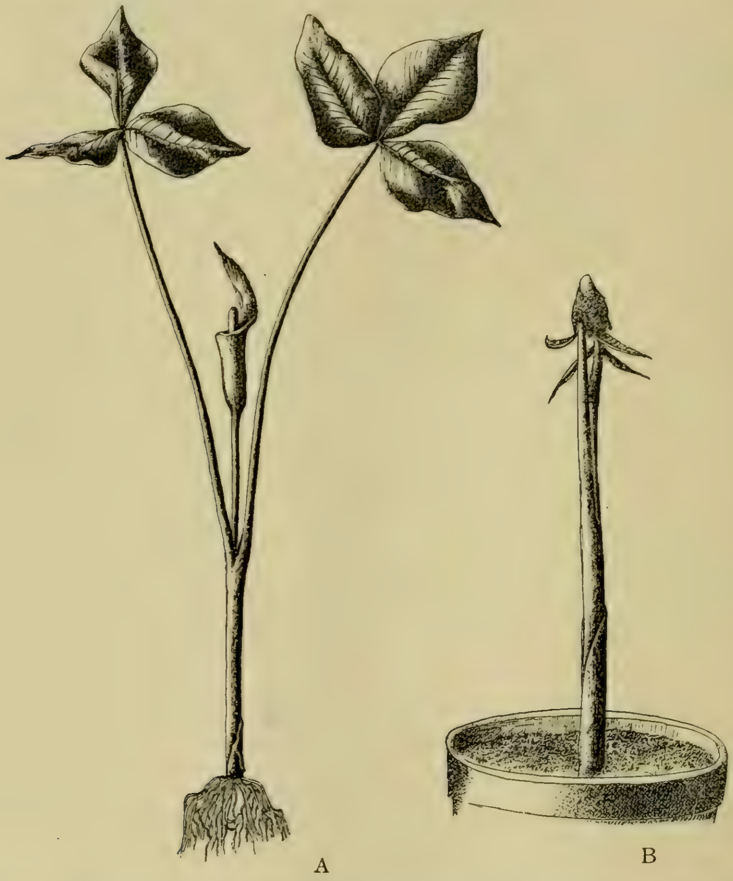

FIG. 12. *Arisaema triphyllum.* *A*, plant grown in portable dark chamber with occasional exposure to diffuse daylight. *B*, etiolated bud shortly after opening: an apical portion of the prophyll is borne on the tips of the leaf.

Roots were not sent out from the crown of the corm until about the time of the maturity of the leaves. The petioles are normally about equal in length, but in etiolated cultures one was often much longer than the other. The laminae did not unfold when the cultures were made in absolute darkness. It was noted, however, that etiolations made in the small portable dark chambers, which were examined daily in an exposure to sunlight for two or three minutes showed a different stature for the leaves. In such instances the laminae were extended in a plane and had a superficial area of about half that of the normal. This result has been verified by repeated observations and suggests that etiolative reactions must be accepted with caution unless known to have been secured in a total exclusion of daylight. This caution takes on special emphasis from the fact that such vitiated etiolations may not show the presence of chlorophyl. Sachs' criterion of perfect etiolation is therefore not one which may be depended upon in all species. (See Fig. 12.)

The scape of the flower showed excessive elongation and the spathe did not reach normal size, the greatest decrease being located in the overarching hood. The spathe retained its reddish and purplish colors in fairly normal depth so far as comparisons might be made. In some instances the hood showed a strong epinastic growth by which it was recurved outwardly, and in nearly all instances it was more or less nearly erected. (See Fig. 13.)

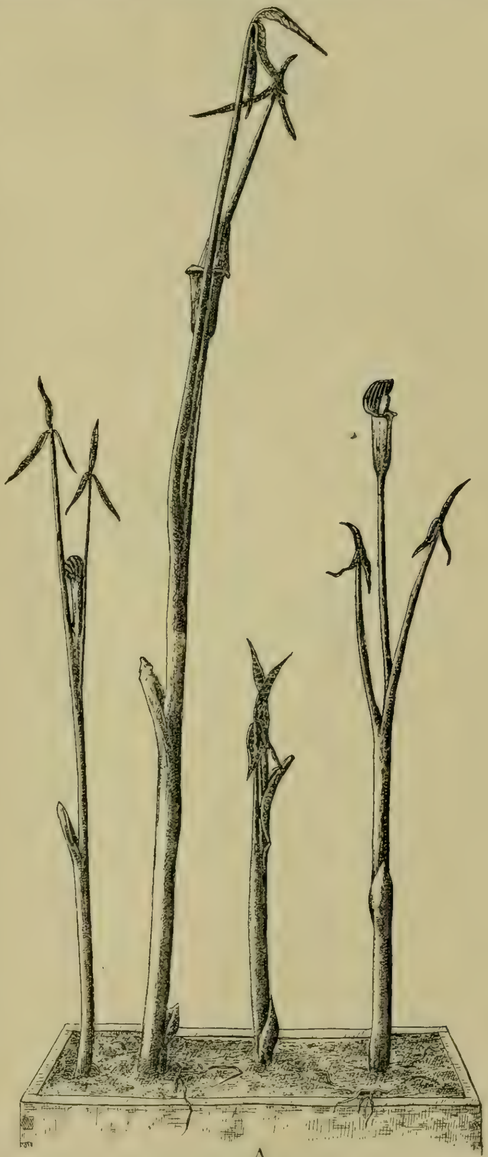

FIG. 13. *Arisaema triphyllum*, grown in almost absolute darkness.

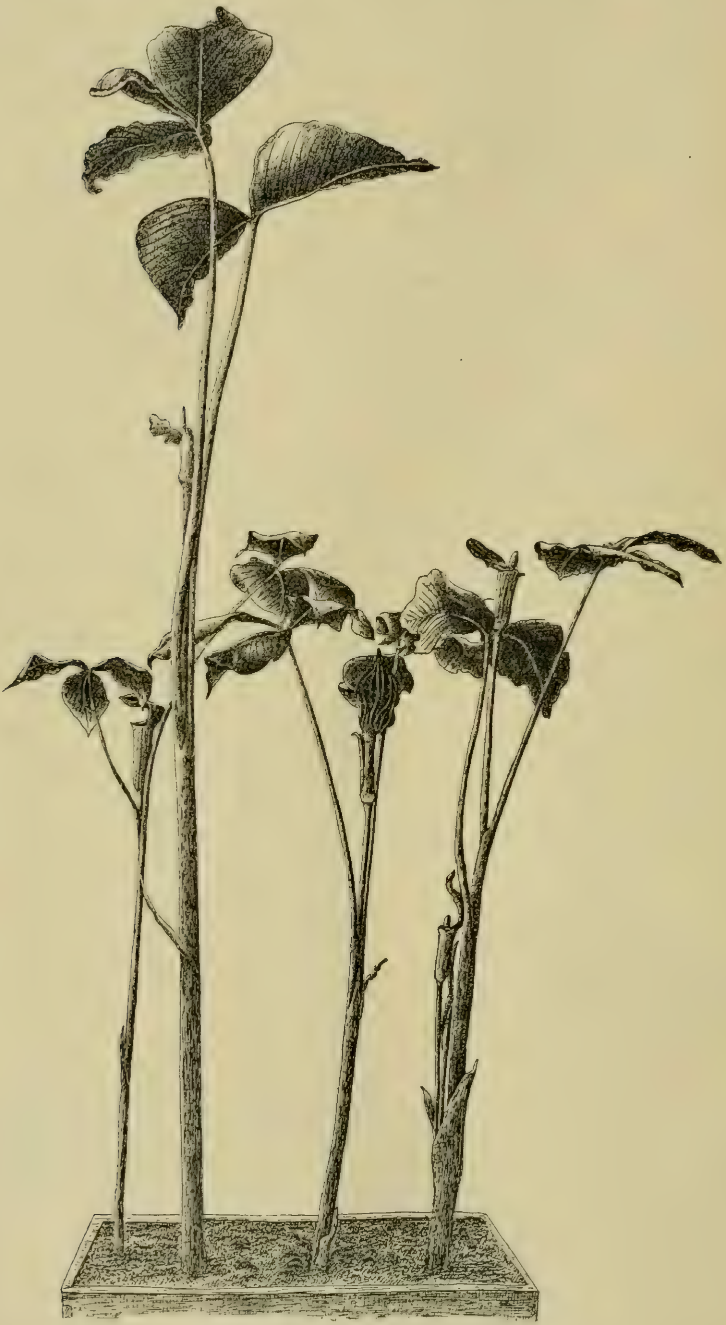

FIG. 14. *Arisaema triphyllum*, showing development of culture in Fig. 13 after exposure to daylight for two weeks.

Stomata were formed in the epidermis of the etiolated prophyll, which were open when examined in water, and the guard cells contained much starch. The length of the epidermal cells in the prophyll was to that of the normal as 18 to 12. Similar relations were found in the epidermis of the petioles, while the epidermal cells of the scape did not differ widely from the normal in measurement. It is to be seen therefore that the excessive elongation of the aërial organs of *Arisaema triphyllum* is accompanied by a multiplication of the epidermal elements, which are of slightly increased size. The surface of the prophyll is covered with rods of waxy exudation in the normal, which are lacking in etiolated specimens. (See Fig. 16.)

Upon the maturity of etiolated aërial organs the plastic material was withdrawn into the corms, which increased by a thin layer above and cut off a thicker layer below, so that upon the ripening of the corms they were smaller than at the beginning of the test owing to the consumption of some of the material in the work of growth and transpiration. The alterations in the chemical composition of the aërial shoots and corms are shown in the analyses given below. After a resting period of a few months the corms might again be started into renewed activity which resulted in the formation of one, or sometimes two leaves only, with no flower. Third and fourth etiolations might be made in the same manner, in which only single leaves of diminishing size were formed. Half of the original number of corms survived the third etiolation, and a small proportion were still alive and apparently sound after the fourth in darkness, but no further growth could be secured from them. It is probable with more attention to cultural details of temperature, especially during resting periods, that even longer endurance to deprivation of illumination might be observed. The resting periods were shortened by the treatment given the plants in such manner that four growths were made in three calendar years.

The repeated growth in the dark was generally in the same terminal bud, but in some instances its destruction would result in the accelerated increase of two of the lateral buds which formed two small corms at the expense of the older one. It was noted in the repeated etiolations that the formation of roots was very sparing, the chief energy of the plant being directed to the construction of petioles.

The germination of seeds in darkness is followed by the formation of an etiolated leaf, which has a petiole longer than the normal and an undeveloped lamina. The leaf quickly perishes and all of the plastic material is withdrawn into the newly formed tuber. Such small tubers may be started into activity after a period of rest, and may form a second leaf which also perishes during the formation of the second tuber or corm. A third growth in darkness might be made, but the corms formed afterward were incapable of further endurance or existence. (See Fig. 15.)

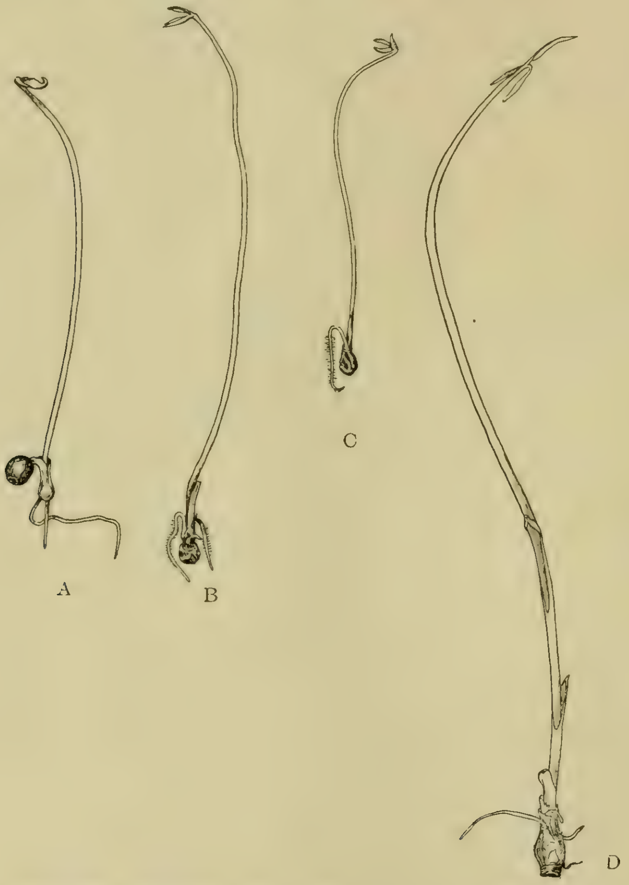

Fig. 15. *Arisaema triphyllum*. *A*, seedling after first etiolation. *B*, seedling after second etiolation. *C*, seedling after third etiolation. *D*, adult plant after fourth etiolation, from corm.

The capacity of *Arisaema* by which it is able to construct leaves both from corms, and from the seedling stage in darkness during three and four successive seasons is a remarkable fact, and is illustrative

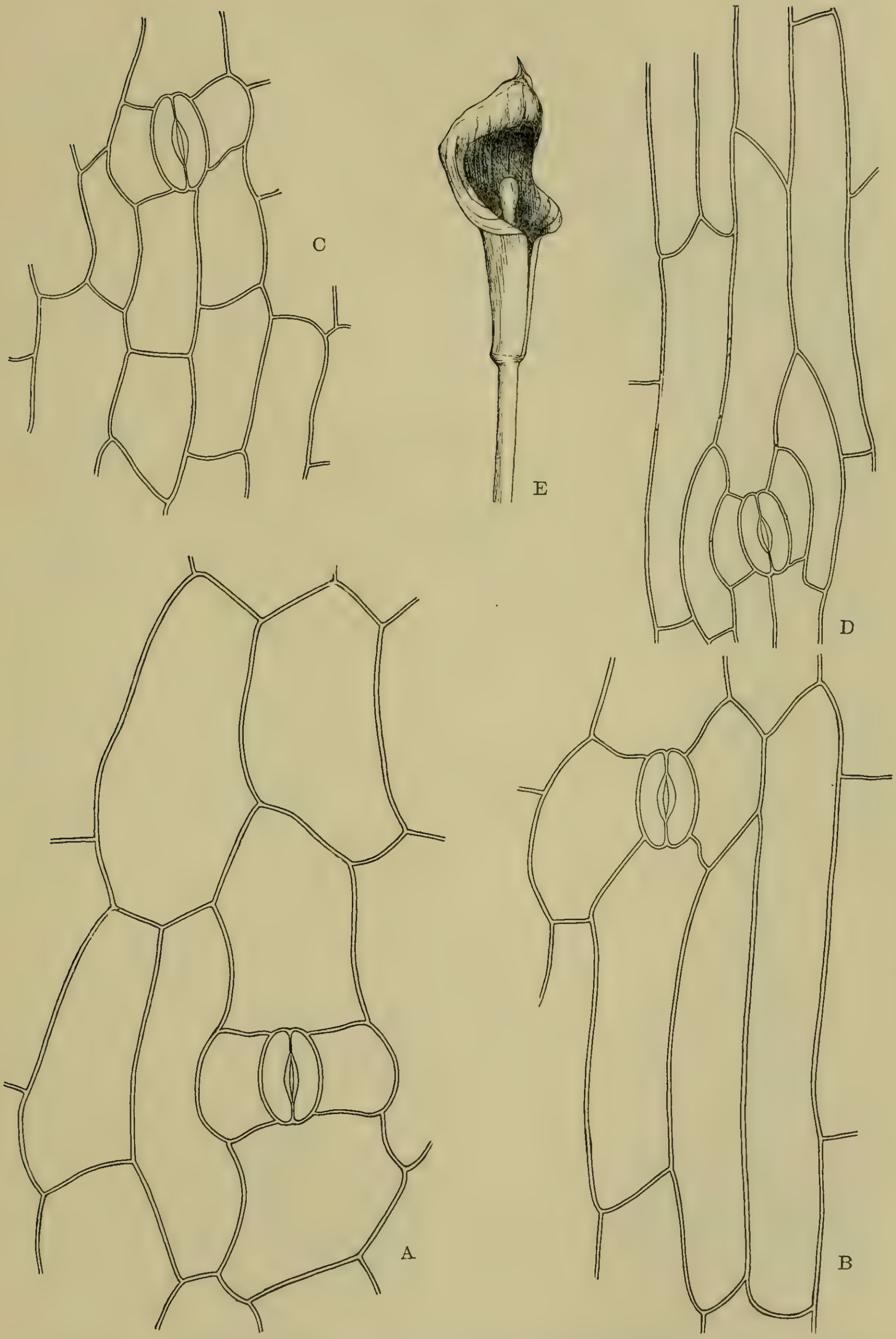

Fig. 16. *Arisaema triphyllum.* *A*, surface view of epidermis of normal petiole. *B*, surface view of epidermis of etiolated petiole. *C*, epidermis of normal prophyll. *D*, epidermis of etiolated prophyll. *E*, etiolated flower.

of the immense reserve energy of plants with storage organs. Such an adaptation would be of great value in plants growing in loose moist soil in woods and meadows. The corms undoubtedly are often covered with soil, humus, or dry leaves to great depths. In such instances the power of excessive elongation of the prophyll would enable the plant to make a strong effort to emerge from such unfavorable conditions, and failing in the first attempt, the trial might be made a second, third; and even a fourth time, with greatly increased chances for survival over the plants which must win the light in the first attempt or perish. (See Fig. 12.)

Cultures were made in very diffuse daylight in which the temperature was exactly the same as of others in direct sunlight. It was found that the petioles did not show an elongation beyond that of the average normal specimen, but the laminae were reduced below the average in superficial area, and assumed a curved position. The overarching hood of the spathe assumed the upright position characteristic of the etiolated cultures. (See Fig. 17.)

A number of studies of the method and rate of growth of the peduncles and petioles were made. To determine the region of maximum elongation, intervals of a centimeter were marked on the petioles and scapes and these intervals remeasured at maturity. The following final lengths show the locations of the greatest growth.

PETIOLE.

Basal,	3 cm.	6	7	12	10.5	4.5	Terminal.

SCAPE.

Basal,	7 cm.	5	4	5	Terminal.

It is to be seen that the greatest elongation of the petioles takes place in a region above the middle, while it is basal in the scape.

Peduncles and scapes have been attached to various auxanometers during the course of the experiments, extending over five years and the results, in so far as to periodicity and maximum elongation, have been fairly uniform. A consideration of the facts thus obtained forces one to the conclusion that the growth of the peduncle and petiole in light is not characterized by any periodicity dependent upon, or influenced by light. The rate of growth was found to increase after 10 A. M. in most instances, or a short time after a rise in the daily temperature customary in greenhouses, which as an after-effect culminated at 6 or 8 P. M. Lesser maxima were induced by unusual variations in temperature. No marked periodicity could be detected in the rate of growth in the dark room kept at a constant temperature although slight fluctuations were seen. Similar irregular fluctuations in the rate were observed in the growth of the prophyll in darkness. The fluctuations in the dark room might be accounted for partly by the daily addi-

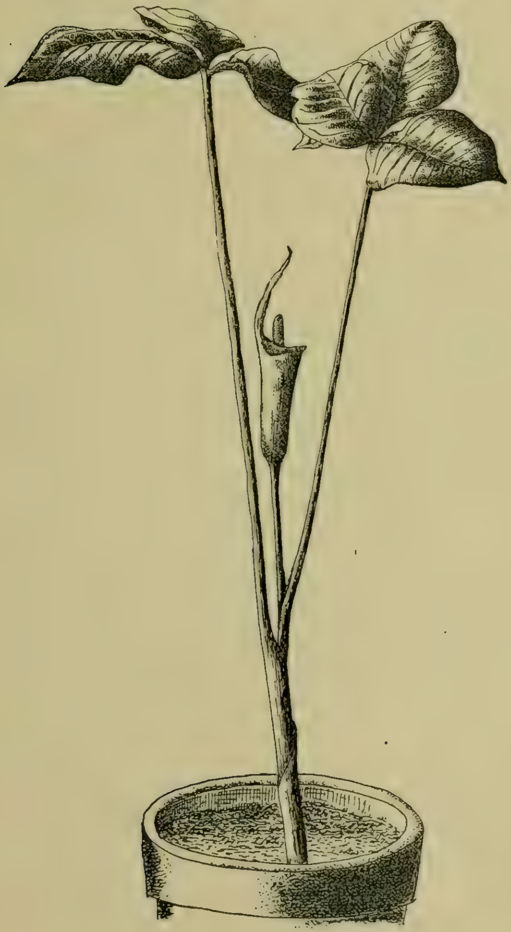

FIG. 17. *Arisaema triphyllum.* Grown in diffuse light.

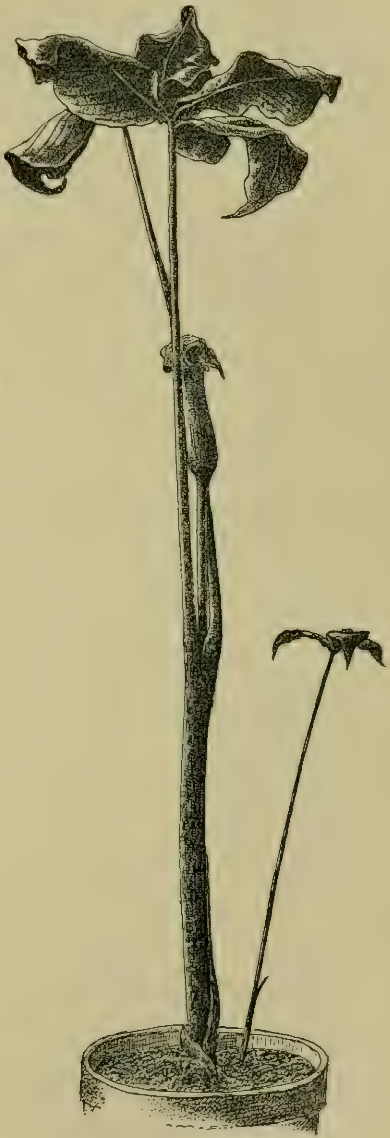

FIG. 18. *Arisaema triphyllum.* Adult plant after confinement in dark room two weeks.

tion of water to the cultures, which was given as the state of the cultures seemed to demand it. The same influence would also be operative in the illuminated cultures. It is therefore certain that *Arisaema triphyllum* does not exhibit a daily periodicity of growth independent of variations in temperature, and that the rate is not notably influenced by light; if light does retard, or accelerate the rate it is masked by the superior influence of temperature and transpiration (see Figs. 19, 20, 22, 23, 24 and 25).

Petioles and scapes which had ceased to elongate at a rate of more than a fraction of a millimeter daily were removed to the dark room when the temperatures of the illuminated room and dark room were equal, and growth was quickly renewed, an elongation of 14 to 16 mm. being made in four or five days. Such additional growth was undoubtedly facilitated by the higher relative humidity of the dark room, but must have been induced by the stimulation of darkness (see Fig. 21).

Etiolated specimens which had attained maturity were brought into a lighted room and found to be capable of expanding the leaflets, which however did not attain the average size of normally developed organs. The erect and recurved hoods of the spathes retained these positions. Variations in the final positions of the leaflets and general aspect of such illuminated etiolations are shown in Fig. 14. In one instance a second flower scape was developed from an etiolated plant after being brought into light.

DETERMINATION OF WATER, DRIED MATERIAL AND ASH.

The following series of determinations were made to ascertain the relative proportion of the main groups of constituents in normal and etiolated material.

I

Resting corms in a dried condition were placed in a moist chamber for a day, after having been out of the soil for three months. The outer dead coats were rubbed off with a cloth, and a corm of medium size with the half of one of the maximum size were weighed, and the various desiccations and combustions gave the following data;

Weight of fresh material	13.995 grams.
" " dried "	3.400 "
" " ash	.108 "

Proportion of water	75·65 per cent.
“ “ dry matter	24·35 “
“ “ “ “ not including ash	24·29 “
“ “ ash in fresh material	·77 “
“ “ “ “ dried “	3·18 “

II

Leaf and petiole of a green plant cultivated in greenhouse;

Weight of fresh material	5·441 grams.
“ “ dried “	·484 “
“ “ ash “	.022 “
Proportion of water in fresh material	91.105 per cent.
“ “ dried matter	8.995 “ “
“ “ ash in fresh material	·404 “ “
“ “ “ “ dried “	4·54 “ “

Corm of Above Plant

Weight of corm	4·243 grams.
“ “ dried material	·532 “
“ “ ash	.013 “
Proportion of water in fresh material	89.84 per cent.
“ “ dried matter in fresh corm	10.16 “ “
“ “ ash in fresh material	·306 “ “
“ “ “ “ dried “	2.44 “ “

III

Etiolated specimens which had been cultivated one year in greenhouse and then forced in dark chamber;

Weight of leaves including petiole and laminae	9·811 grams.
“ “ dried material	.687 “
“ “ ash	.051 “
Proportion of water in fresh material	93·00 per cent.
“ “ dried matter	7·00 “ “
“ “ ash in fresh material	·519 “ “
“ “ “ “ dried “	7·43 “ “
Weight of half of corm of above plant taken when leaves reached maturity	22.00 grams.
Weight of dried material	3·850 “
“ “ ash	.063 “
Proportion of water in fresh material	82.50 per cent.
“ “ dried matter	17·50 “ “
“ “ ash in fresh material	.286 “ “
“ “ “ “ dried “	1.633 “ “

IV

Air-dried seeds collected from fruits grown on plants in the open were cleaned and dried in air at ordinary temperatures;

Weight of material	3.619 grams.
“ “ dried matter	3.320 “
“ “ ash	.059 “
Proportion of water	8.27 per cent.
“ “ dried matter	91.73 “
“ “ ash in fresh material	1.63 “
“ “ “ “ dried “	1.77 “

V

Determination of the constituents of an entire etiolated plant during its second growth in darkness;

Weight of corm	9.927 grams.
“ “ dried material	.796 “
“ “ ash	.045 “
Proportion of water	80.18 per cent.
“ “ dried matter	19.82 “
“ “ ash in fresh material	.453 “
“ “ “ “ dried “	5.89 “
Weight of entire single leaf with petiole	4.916 grams.
“ “ dried material	.185 “
“ “ ash	.018 “
Proportion of water	96.24 per cent.
“ “ dried matter	3.76 “
“ “ ash in fresh material	.366 “
“ “ “ “ dried “	9.73 “

VI

Determination of constituents of three seedlings during the second season of development;

Weight of corms	1.229 grams.
“ “ dried material	.302 “
“ “ ash	.005 “
Proportion of water	75.43 per cent.
“ “ dried matter	24.57 “
“ “ ash in fresh material	.407 “
“ “ “ “ dried “	1.655 “

Weight of leaves	3.639	grams.
" " dried material	.392	"
" " ash	.009	"
Proportion of water	89.23	per cent.
" " dried matter	10.77	"
" " ash in fresh material	.247	"
" " " dried material	2.28	"

VII

Determination of constituents of small plant grown in very diffuse light;

Weight of fresh leaves including petioles	6.56	grams.
" " dried material	.384	"
" " ash	.020	"
Proportion of water	94.33	per cent.
" " dried matter	5.67	"
" " ash in fresh material	.305	"
" " " " dried "	5.20	"
Weight of corm	2.834	grams.
" " dried material	.557	"
" " ash	.025	"
Proportion of water in fresh material	80.70	per cent.
" " dried matter	19.30	"
" " ash in fresh material	.882	"
" " " " dried "	4.41	"

VIII

A number of seeds of an average weight of .03585 g. were placed in the soil on January 2, 1899, and after the tubers formed from the seedlings grown in darkness were fully mature, and the leaf had perished, the following determinations of the constituents of the corms were made;

Weight of fresh material	.13	gram.
" " dried "	.024	"
" " ash "	.001	"
Proportion of water in fresh material	88.4	per cent.
" " dried matter	11.6	"

IX

Determination of constituents of four corms grown from seeds germinated in light, and the leaves allowed to come to maturity and perish;

Weight of fresh material	.201	gram.
“ “ dried “	.049	“
“ “ ash “	.002	“
Proportion of water in fresh material	75.3	per cent.
“ “ dried matter	24.7	“

X

Determination of the composition of seeds;

Weight of 25 air-dried seeds	.851	gram.
“ “ dried material	.762	“
“ “ ash	.016	“
Proportion of water	10.46	per cent.
“ “ dried matter	89.54	“
“ “ ash in fresh material	1.88	“
“ “ “ dried “	2.09	“

It is to be seen by a consideration of the above data that the resting corm of a plant, which has been etiolated once, contains a greater proportion of water and less dried material than the normal, a relation that holds during the second etiolation also. The proportion of ash in the fresh material in etiolated corms was found to be less than in the normal, while the proportion of ash to the other constituents of the dried matter increased by reason of the actual decrease of the latter. The proportion of water in etiolated leaves was greater than the normal, and the proportion of ash in the fresh material less, in the corm. Likewise the proportion of ash to the other constituents of the dried matter was very much greater than in the normal.

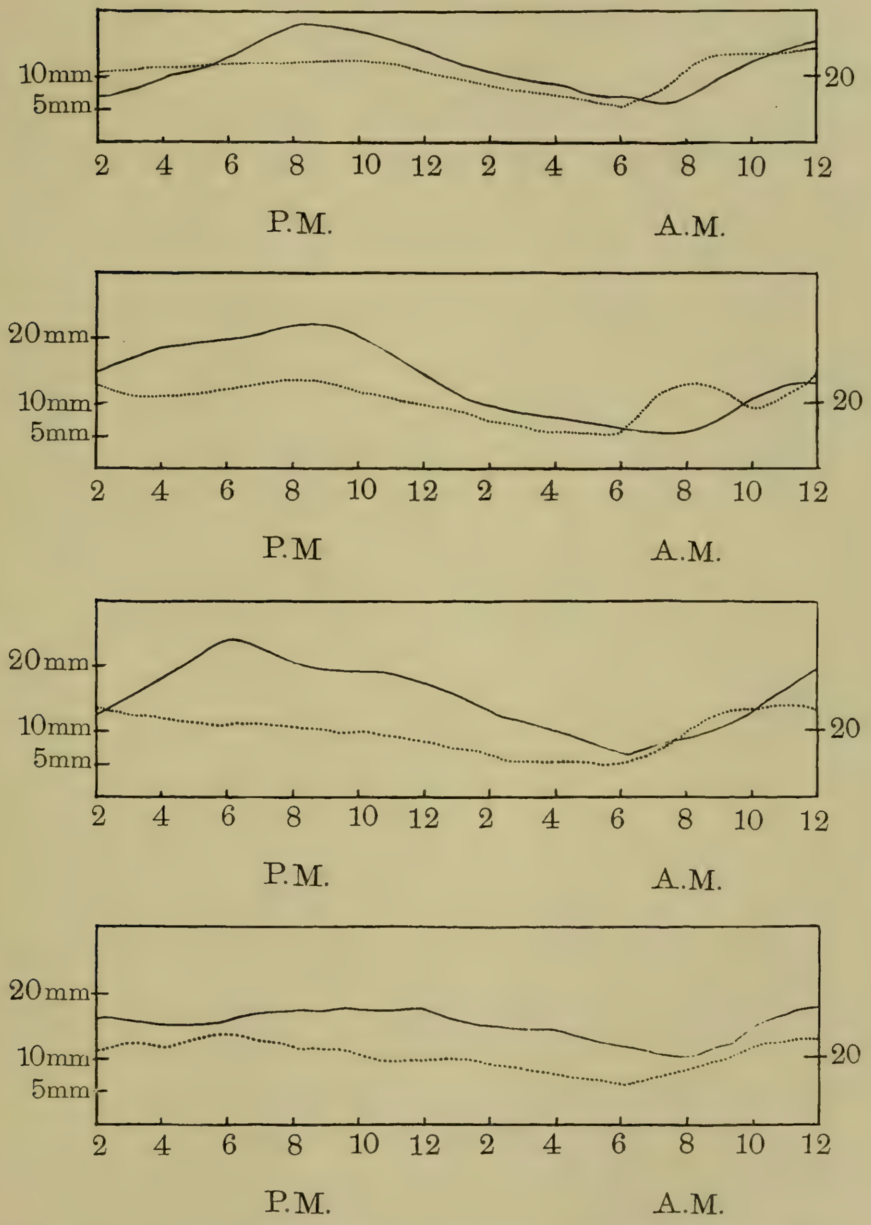

FIG. 19. Curve of growth of scape of *Arisaema triphyllum* under normal illumination, March 26 to 30, 1901. (See Fig. 20.) Description on p. 67.

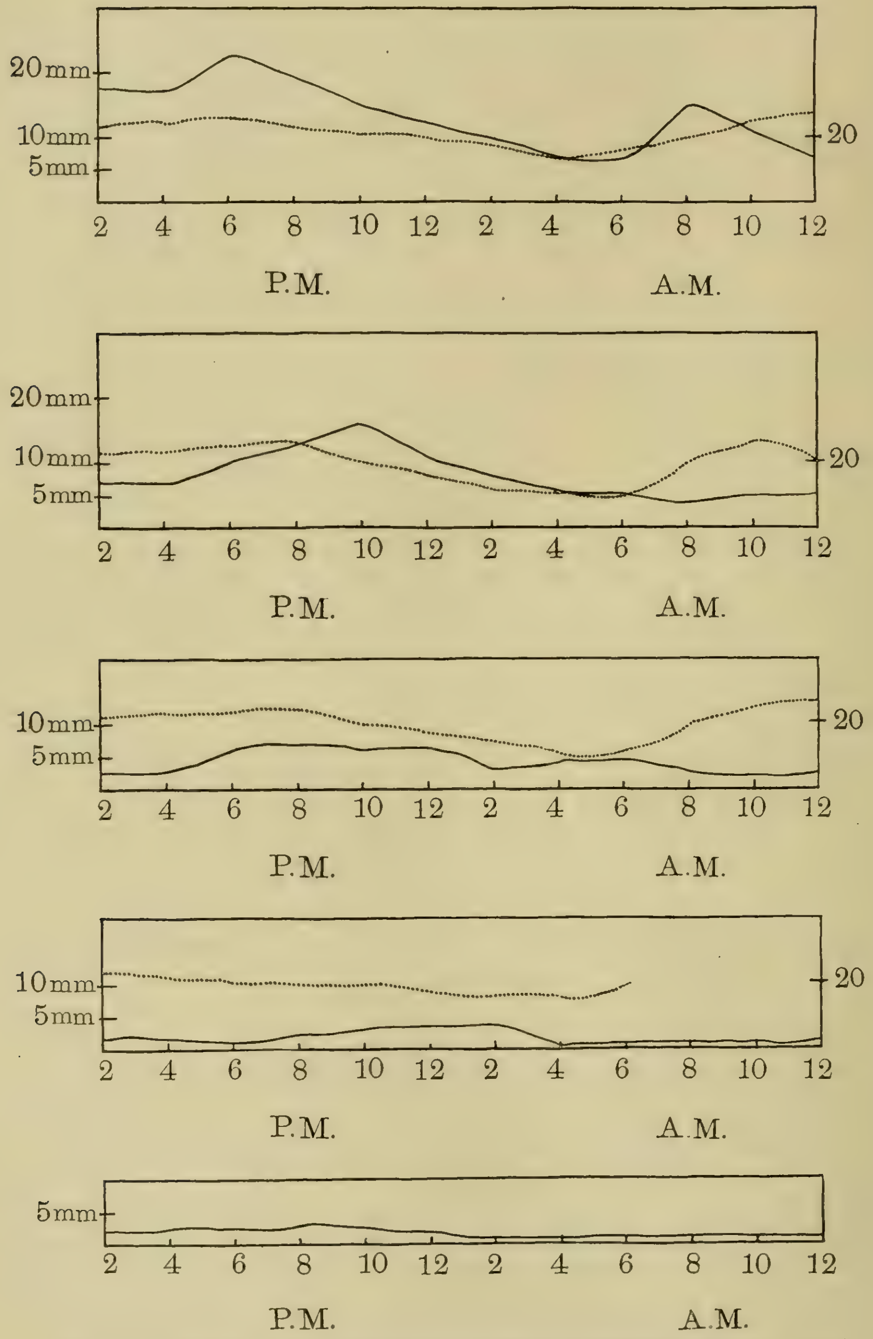

FIG. 20. Curve of growth of scape of *Arisaema triphyllum*, March 30 to April 5, 1901. (Continued from Fig. 19.) Description on p. 67.

Comment on Figs. 19 and 20. The rate of growth of the scape is represented by the continuous line and the actual elongation during every period of two hours is denoted by half the distance of this line from the base line measured from the point over the numerals denoting the hours. 5, 10 and 20 millimeter intervals are marked on the left hand margin for convenience. The course of temperature is designated by the dotted line, and the single reference point of 20° C. is marked on the right hand margin of the plans. The temperature is seen to range from 15° to 25° C., and the maximum rate of growth of about 11 mm. for the two-hour period ending at 6 p. m. on March 30. During the last 12 hours of the observations the total amount of growth did not exceed 3 mm. and the preparation was removed to the dark room with the result that an immediate acceleration of growth was shown as illustrated in Fig. 21.

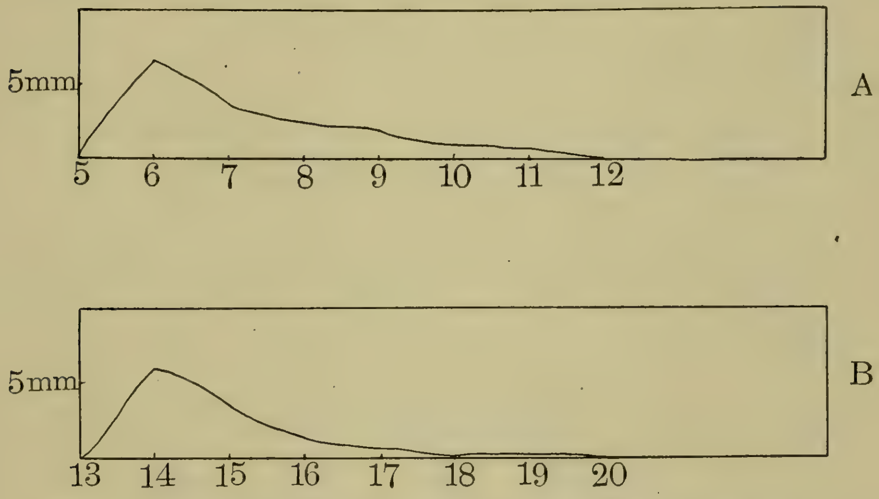

Fig. 21. *A*, curve of growth of normal peduncle placed in dark chamber at constant temperature of 19 to 21° C. Maximum rate of elongation of 3 mm. in a 2-hour period was shown. *B*, curve of growth of a normal petiole, fully grown, then placed in dark room as in *A*.

Comment on Figs. 22 and 23. The curve of growth is represented by the irregular continuous line and was plotted from auxanometric measurements beginning when the sheathing prophyll had attained a length of 10 cm. and could be opened to allow the attachment of clamp of a Corbett auxanometer (see MacDougal's Practical Text-Book of Plant Physiology, p. 287. 1901). The actual amount of

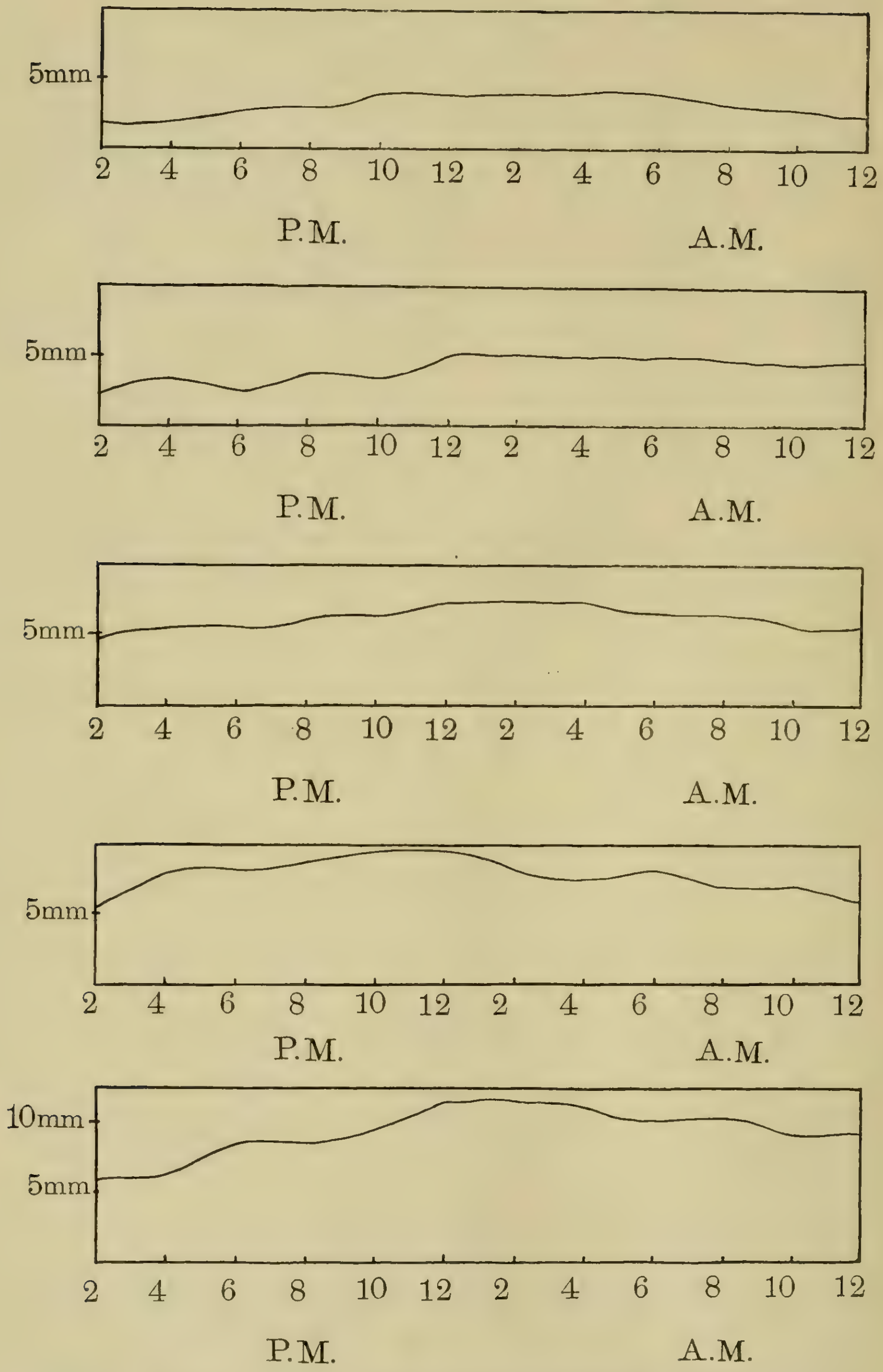

FIG. 22. Curve of growth of scape of *Arisaema triphyllum* in dark room at constant temperature of 17 to 19° C. (See Fig. 23.)

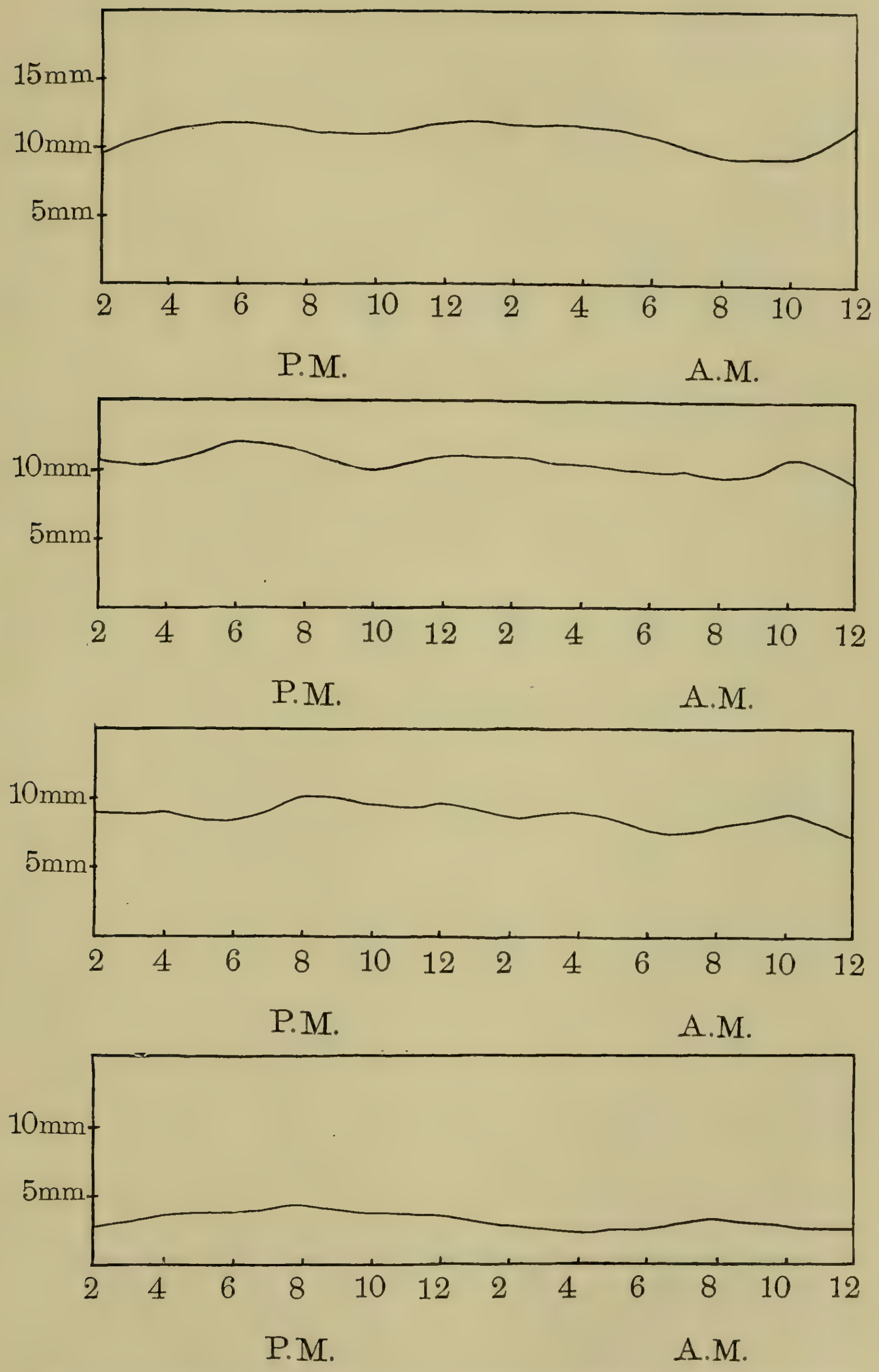

FIG. 23. Curve of growth of scape of *Arisaema triphyllum* in dark room at constant temperature of 17 to 19° C. Continued from Fig. 22. (See Fig. 24.)

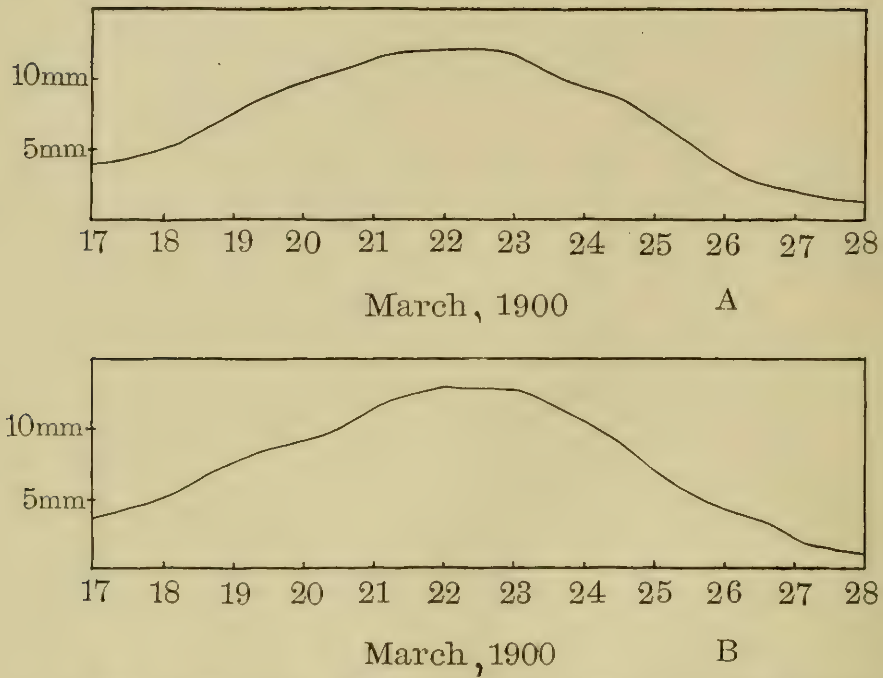

FIG. 24. *A*, grand period of growth of etiolated scape of *Arisaema triphyllum* plotted from daily maximum rate. *B*, grand period of growth plotted from total daily amount of growth.

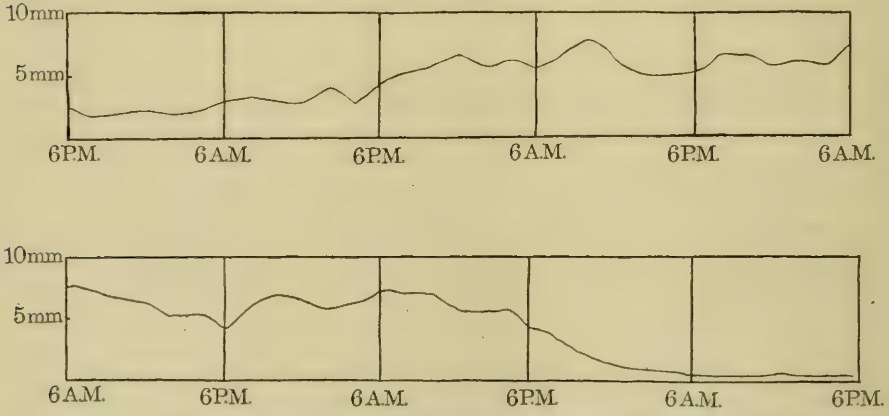

FIG. 25. Curve showing rate and amount of growth of prophyll of *Arisaema triphyllum* in dark chamber. The measurements were begun when the prophyll had reached a length of 3 cm. and ended five days later when it had ceased to elongate at a length of 35 cm. The distance from the base line to the curve denotes the actual amount of growth during the two-hour periods, the maximum being about 4 mm. per hour. The temperature of the dark room was 22° C. at the beginning of the observations and gradually fell to 20° C. near the end.

growth during any two-hour period may be found by taking half the distance of the curve from the base line from a point over the numeral denoting the end of the period. Elongation continued three days later than the plotted record.

Aristolochia sp.

Some tubers of *Aristolochia* brought from Bermuda in 1900 were placed in the propagating house after a proper period of rest in February, 1901. As soon as indications of activity were shown two cultures were removed to the dark room.

The normal stems attained a length of 18 to 25 cm. with internodes 1.5 to 3 cm. long. The laminae of the cordate leaves measured 2.5 by 4 cm. with petioles 1 to 2 cm. long, in the normal specimen. The normal petioles were curved downward throughout their entire length, but most sharply near the laminae in such manner as to bring the outer (lower) surface of the leaf uppermost, at an angle of 45° with the vertical. The etiolated stems on the same date were about 15 cm. long and upright. Later the normal stems began to show marked movements and twine about supports while the etiolated stems became weak and dependent, finally reaching a length of 1.7 meters, far in excess of that of the normal at a much later stage.

The terminal portion of etiolated stems remained apogeotropic and the internodes attained a length of 2.5 to 6 cm., showing a marked increase above the normal. The petioles were 5 and 6 cm. in length, which is also much more than the normal. The etiolated petioles assumed an angle of about 38° with the stem, and did not exhibit any form of geotropic response. The laminae were folded together with the upper (inner) faces appressed. The number of stomata on etiolated examples was much less than in the normal.

The etiolated stems attained a greater diameter than the normal, due chiefly to exaggeration in the size of the elements in the cortex and pith. The heavy thickening of the walls of the cortex and epidermis of the normal was notably lacking in etiolated specimens. The pericycle was notably thinner, with the elements less heavily pitted. The entire stele remained in an embryonic condition and the cambium was much less strongly developed than in the normal. The tubers were allowed to become dry and go into a resting stage in the dark room in June, 1901. In December a second etiolated growth ensued, which did not differ greatly from the first season's activity. Many tests were made with supports and other objects brought into contact with the apical portions of the stems, but in no instance did

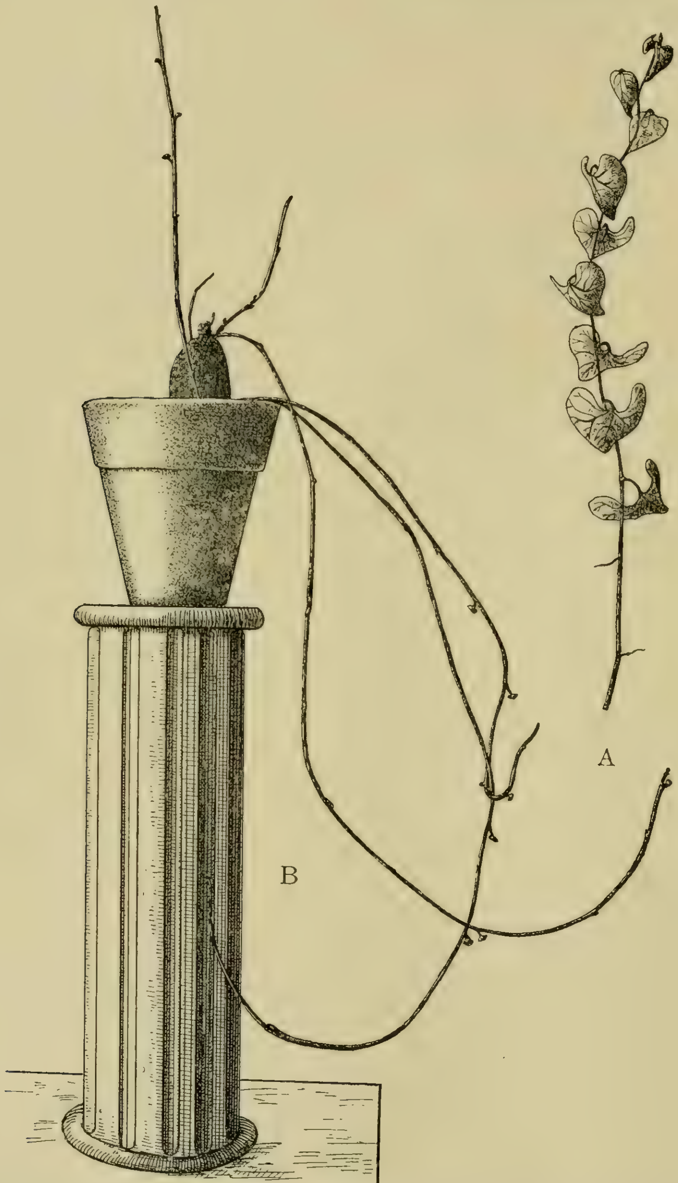

FIG. 26. *A*, terminal portion of normal stem of *Aristolochia*. *B*, etiolated culture of *Aristolochia*.

twining occur, a result in accord with tests with all other etiolated climbers. The second etiolation did not exhaust the tubers, and *Aristolochia* is to be added to the list of species capable of several efforts to reach sunlight while being nourished from storage organs.

Asparagus officinalis L.

Clumps of *Asparagus officinalis* in a resting condition were placed in the dark chamber in October, 1901, and soon began to send up stems. The normal cultures in the greenhouses formed shoots about a meter in height, with many branches, the branches being subdivided and bearing many cylindrical cladodes. Etiolated stems attained a diameter about double that of the normal, being about the same thickness as the underground portion of normal cultures, but having much longer internodes. The internodes of normal and etiolated stems were about equal. Branches were sent out by only a few of the etiolated stems, generally by those which had fallen prostrate after a growth of about .7 of a meter. The branches were thicker than the normal and attained a length of about 10–15 cm., and were not subdivided. The terminal portion of the stem retained its apogeotropism and curved upward when the stem had fallen by reason of its mechanical weakness.

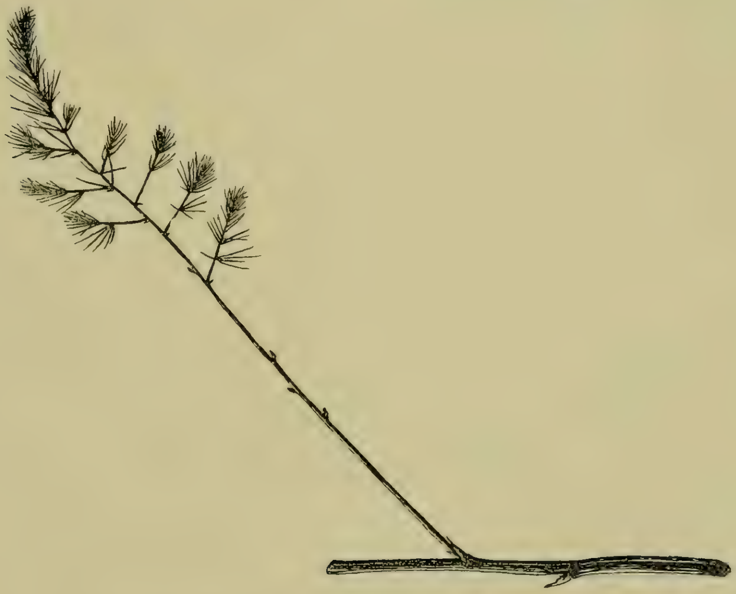

FIG. 27. Portion of normal stem of *Asparagus officinalis* with branch and cladode.

The true leaves, which appear as bracts subtending the cladodes, were somewhat larger in the etiolated examples, and are almost pure white in color.

Normal stems show a very irregular outline in transverse section due to the unequal thickness of the cortex, which is not fully illustrated by Fig. 29. The etiolated stems are variously compressed from a cylindrical form, but the curves in the cross-section are not so sharp or crooked. The cells of the etiolated epidermis are somewhat elongated, and this layer is furnished with stomata apparently functionally normal. The epidermal cells are larger in all transverse diameters than the normal and the outer wall lacks the outer thickening layer. The etiolated cortex is also composed of much larger elements than the normal, which assume more rounded forms, and are furnished with greater air-spaces. The walls of the normal cortex are much heavier than in the etiolated. The marked increase in the diameter of the etiolated stem is to be attributed chiefly to the exaggeration of the cortex, although the fundamental parenchyma may participate to some extent in the matter. It is noticeable, however, that the central lysigenous cavity of the normal stem is lacking in etiolated organs. The normal stem has a heavy pericycle

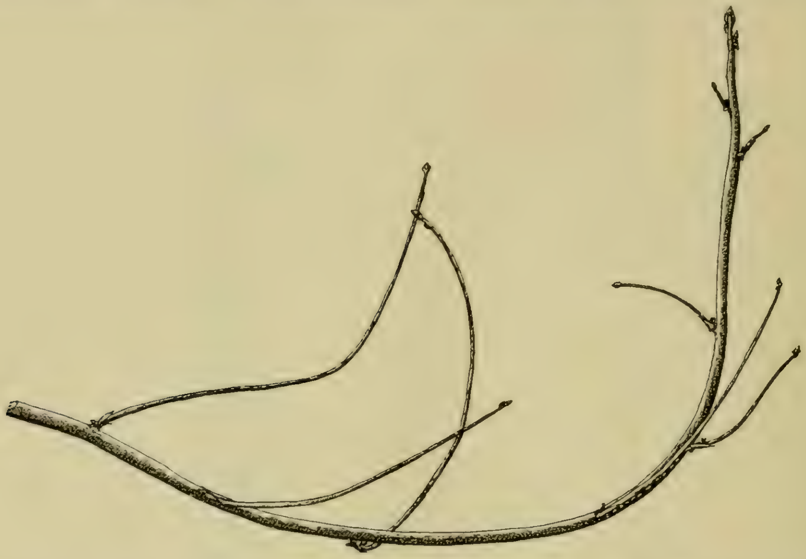

FIG. 28. Terminal portion of etiolated shoot of *Asparagus officinalis* with branches. This shoot has fallen prostrate and the apex has curved upward geotropically.

with walls thickened to such an extent as to almost obliterate the lumina in same instances. The etiolated stem presents a marked contrast in this matter. Only four or five layers of the pericycle are noticeably thickened and the walls have but a fraction of the diameter of the normal. The steles in the central portion of the etiolated stems showed least departure from the normal. Those lying externally, however, remained in a primitive stage of development. The spiral vessels were best differentiated, while the great annular vessels had very thin walls. The sieve tissues also showed a lack of differentiation, and their contents were not so dense as in the normal.

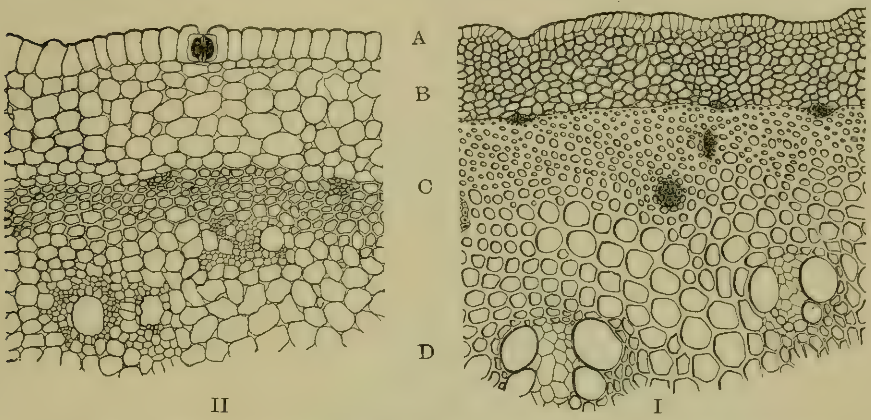

FIG. 29. I, partial transverse section of normal stem of *Asparagus officinalis*. II, partial transverse section of etiolated stem. *A*, epidermis. *B*, cortex. *C*, pericycle. *D*, region in which large bundles are seen.

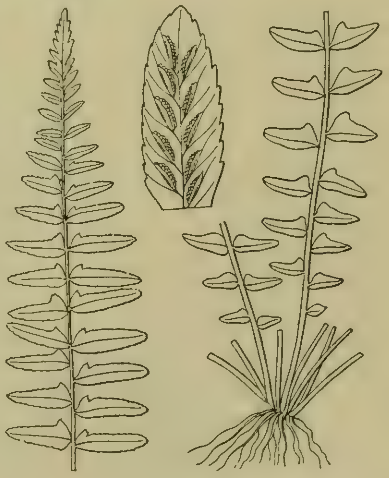

FIG. 30. *Asplenium platyneuron.* Normal. After Britton and Brown.

Asplenium platyneuron (L.) Oakes.

Rhizomes collected at New Canaan, Conn., November 27, 1900, were placed in the dark room at once, and showed indications of activity within a few weeks. Fronds curved in the form of an open spiral of one and a half revolutions with a midrib 20 cm. long were

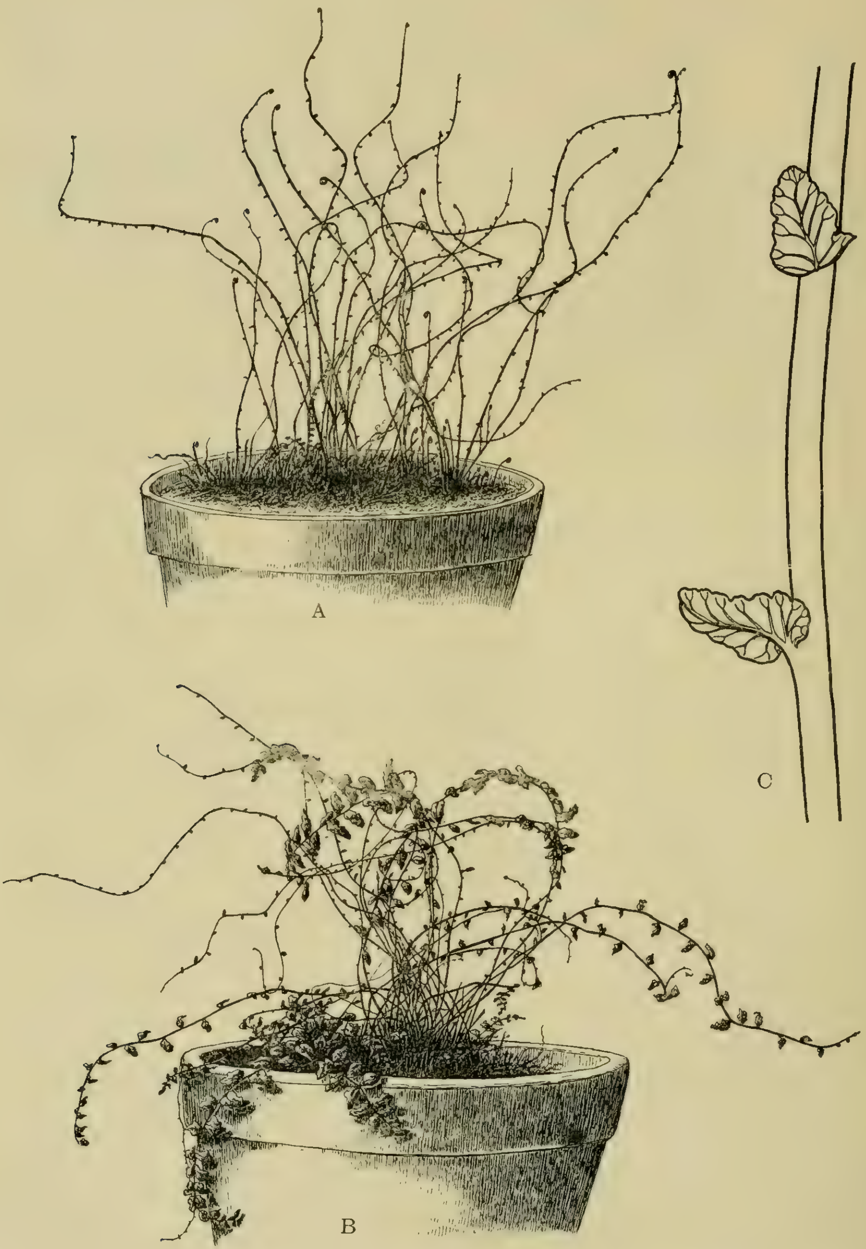

FIG. 31. *A*, etiolated culture of *Asplenium platyneuron*. *B*, same after illumination for ten days. *C*, portion of midrib with pinnae, × 4.

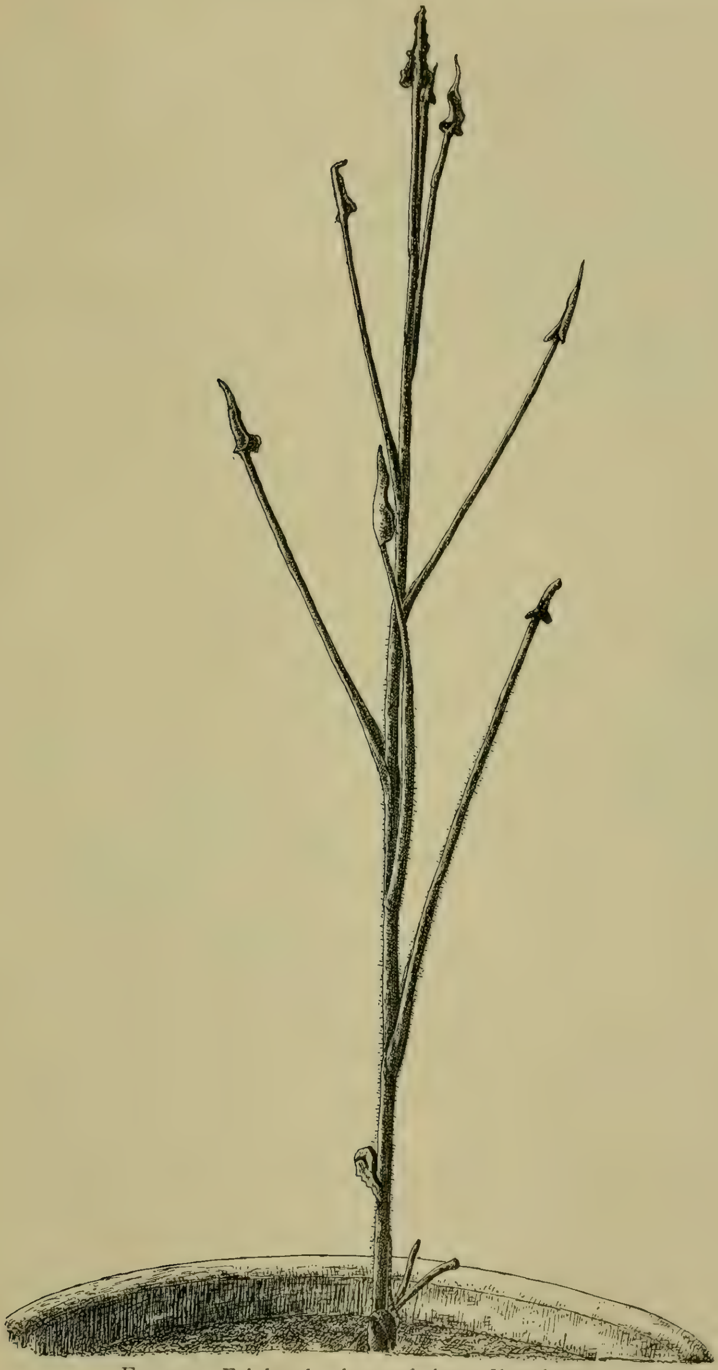

FIG. 32. Etiolated culture of *Aster divaricatus*.

formed by March 6, 1901. The midrib was about a millimeter in diameter midway between the tip and base. The pinnae were represented by flattened expansions 1.5 by 1 mm. with oblique auricled basal lobes. Later three or four pairs of lobes could be made out in the pinnae. The lower (outer) surfaces of the pinnae showed numbers of stomata with a circular outline, which were slightly open when examined in water. The guard cells, as well as the spongy parenchyma, were richly loaded with chloroplasts containing chlorophyl, and the entire plant above the soil has a decided green color.

An examination of the structure of the pinnae revealed the fact that the fibrovascular tissues were in a very primitive stage of development. The mesophyll were but slightly differentiated, and intercellular spaces were very sparse.

An etiolated culture was brought into the light on April 2, and the older pinnae underwent but little structural change except in the formation of additional chlorophyl. Pinnae of the younger fronds, which had accomplished but little growth at the time of illumination attained a stature more nearly that of the normal, and the differentiation of the tissues was carried out in much the usual manner. It is to be noted also that such pinnae stand much farther apart than the normal, showing an excessive elongation of the midrib.

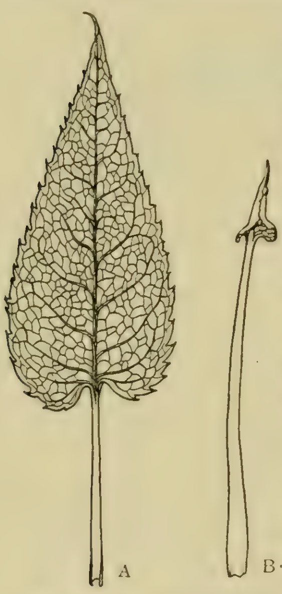

FIG. 33. *Aster divaricatus. A*, normal leaf. *B*, etiolated leaf.

Aster divaricatus L.

Rootstocks of *Aster divaricatus* were brought into the dark room in February, 1900, and soon showed a rapid growth of the shoot. Etiolated stems attained a height of about 35 cm. which is not far from the average of the normal plant. Fifteen leaves were formed on a typical specimen, with petioles about 5 to 6 cm. long. The laminae were about 2 cm. long and 1 cm. wide when unrolled. The upper surfaces (inner surfaces) remained appressed together, only partially separating in a few instances. The petioles held a position from 30 to 40° from the vertical, or rather from the stem. The hairs on the normal stems were equally abundant on etiolated organs.

Normal stems have several collenchymatous subepidermal layers.

But one or two layers of subepidermal tissue were thickened in the etiolated culture, and only to a slight extent. The intercellular spaces were quite as well marked in etiolated cultures as in normal. The bast fibers were only slightly thickened and no cambium layer was formed in etiolated cultures. Full differentiation of the sieve cells was not accomplished. The bundles are separated by wide primary medullary rays, and the formation of secondary tissues had not begun in etiolated stems. The xylem shows a development arrested before the vessels had reached normal condition, and the pith lacked some of the intercellular spaces found in the normal. Etiolated shoots did not survive very long and the earlier leaves quickly disappeared before the older ones were formed.

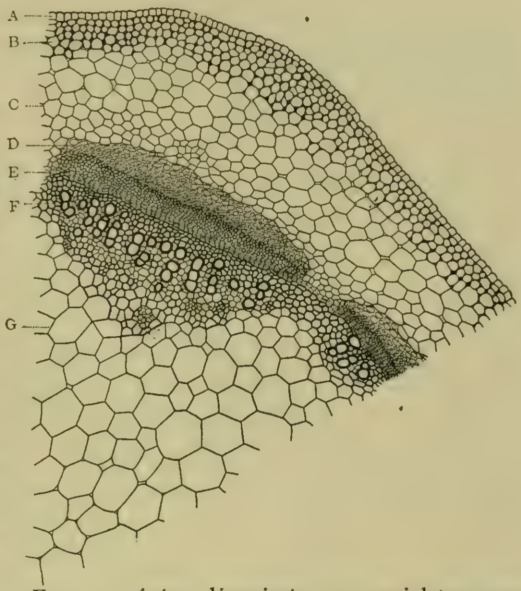

FIG. 34. *Aster divaricatus.* 1, partial transverse section of normal stem. 2, partial cross-section of etiolated stem. *A*, epidermis. *B*, collenchymatous tissue. *C*, cortex. *D*, bast fibers. *E*, cambium. *F*, xylem. *G*, pith.

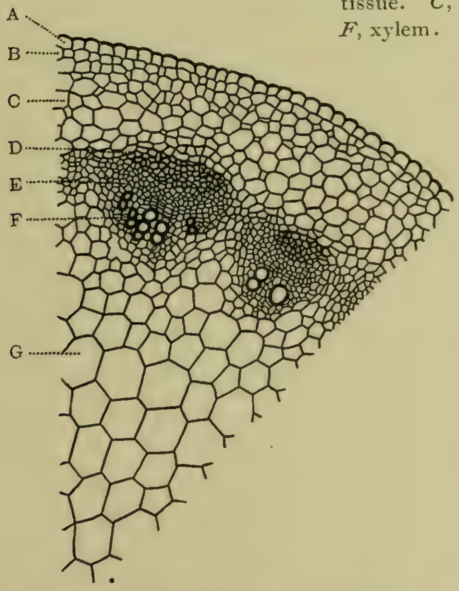

FIG. 35. *Aster divaricatus.* Partial transverse section of etiolated stem. Description as in Fig. 34.

Results similar to the above were obtained from an unknown species which was cultivated later.

Baccharis halimifolia L.

A number of shrubs of *Baccharis* were brought from salt marshes of Staten Island, in November, and placed in the greenhouses and dark chambers. These shrubs were about 140 cm. in height. Within a month a number of the buds about the base of the main stems began to grow and developed slender etiolated stems, which bore small lanceolate leaves and which attained a length of a few centimeters and then perished.

Bicuculla cucullaria (L.) Millsp.

A number of the scaly bulbs of *Bicuculla* were placed in soil in the dark room in January, 1900, and soon showed leaves. The petioles attained a length of 10 to 18 cm., and the terminal portion immediately below the lamina was curved through a complete revolution in such manner that the undeveloped compound lamina was held in a position varying between the inverted vertical and horizontal. The new bulbs formed at the bases of such etiolated leaves were only half the size of the normal, and were entirely free from coloring matter. No unfolding of the compound lamina was shown and the leaves soon perished. A second growth could not be induced.

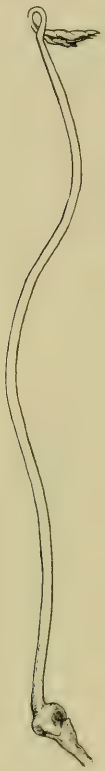

FIG. 36. Etiolated leaf of *Bicuculla* with bulbous enlargement at base.

The average length of the epidermal cells of the etiolated petioles was double that of the normal. The palisade tissue on the upper (inner) side of the laminae could be distinguished, but the remainder of the parenchymatous tissue was closely packed, and no stomatal organs were found, a fact in correlation with the short duration of the etiolated leaf. The width of the epidermal cells remained exactly the same in etiolations and the increase was shown wholly in length.

Botrychium obliquum MUHL.

Rootstocks of *Botrychium* were placed in the dark room in October, 1899. The stipe attained a length of 18 cm. below the point where it divided into two branches, one of which was again divided, at a distance of 1.5 cm. The three branches thus shown were 9, 10, and 16 cm. in length respectively, and only the larger one developed lateral branches of noticeable size, but all had a cluster of foliar rudiments at the extremities of the pinnae.

A spore-bearing pinna usually arises from the stipe near the point where it branches, but in the etiolated cultures this organ was represented by an atrophied structure near the base of the stipe. The stipe was much longer than the normal, and the excessive growth was seen to take place in the upper part of the main stalk and in the adjacent bases of the branches. The diameter of the stipe was something greater than that of the normal organ.

The upper portion of the stipe has two schizosteles of crescentic cross-section with the concavities facing each other in the normal, and distinctly separated by masses of fundamental parenchyma. The etiolated stipe had two large schizosteles almost confluent at the margins in much the same manner as the structures in the basal portion of the normal main stipe.

The thickening of the normal epidermis is noticeably lacking in the etiolated stipe. The parenchymatous cells are slightly larger and with thinner walls in the etiolated specimens. The sclerenchymatous tissue shows but little thickening in the etiolated stipes, and a similar lack of development is to be seen in the xylem, in which the walls are hardly half the diameter of the normal.

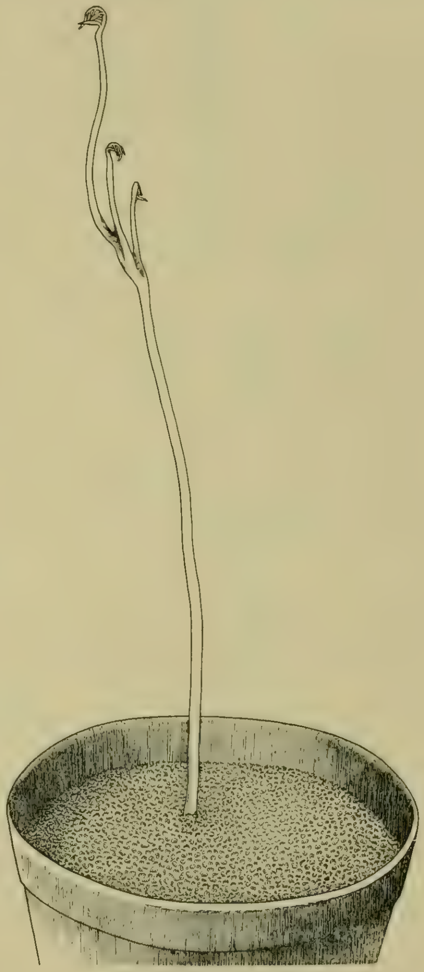

Fig. 37. Etiolated culture of *Botrychium obliquum*.

Stomata, which are open when examined in water, are present in etiolated stipes, and the epidermal cells are excessively elongated, showing a length of 20 as compared with 12 in the normal examples. In this instance the epidermal cells appear to keep pace with the excessive growth of the stipe, although such correlation is of doubtful significance. Some chlorophyl was present, giving the etiolated specimens a distinct green color, in accord with the behavior of all other ferns examined. Torsions were observed in the stipes of all etiolated examples of *Botrychium*. It was also noticeable that the midribs of the pinnae were thicker than in the normal. The grooves usually present on the upper surfaces of normal midribs were lacking in etiolated specimens.

Bowiea volubilis Harv.

Bowiea volubilis is a singular type of a xerophyte. It forms a large bulb with heavy green scales, from the central axis of which usually arises a scape 1 to 2 meters in length, bearing small liliaceous flowers. The base of this aërial shoot is usually sheathed with two or three small bract-like leaves which arise from it at points below emergence from the scales.

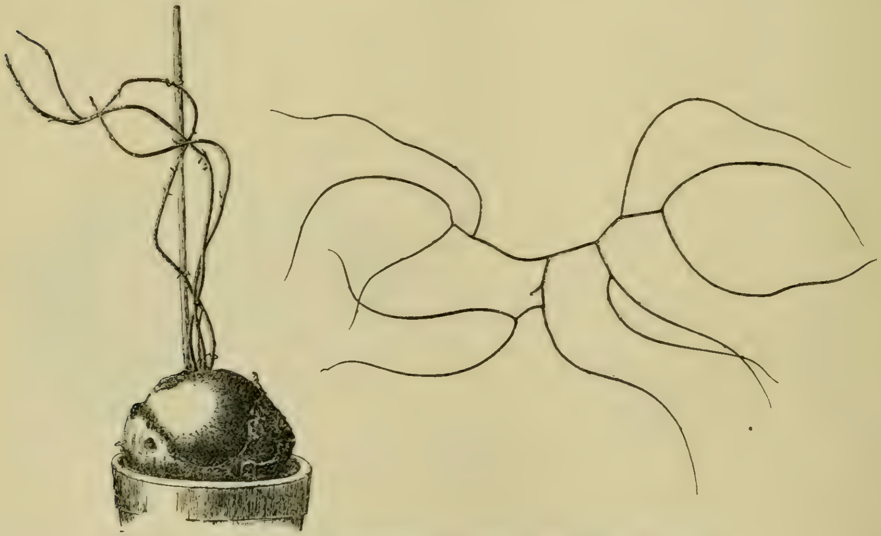

FIG. 38. Etiolated culture of *Bowiea* and normal branch.

Bulbs, which had rested properly during the summer of 1900, were placed under cultural conditions in the dark chamber in September. Three shoots were sent up from a single bulb, reaching a

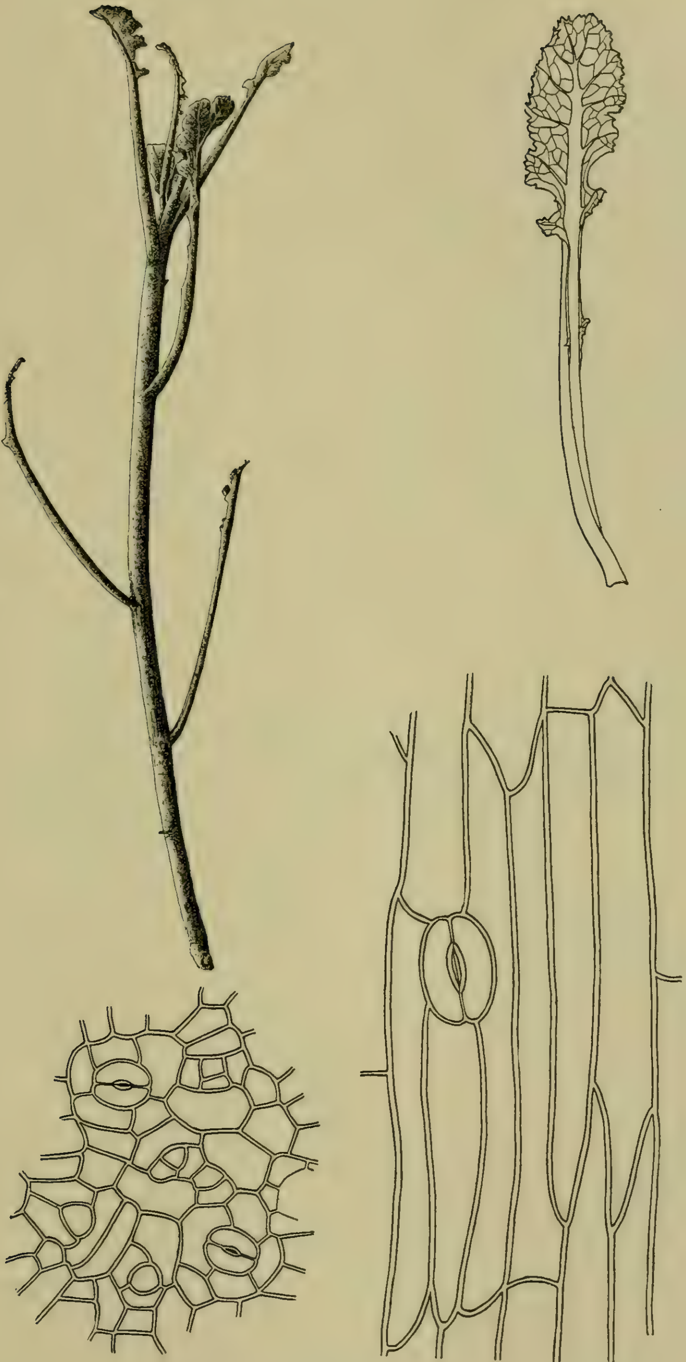

FIG. 39. *Brassica campestris.* Etiolated shoot, single leaf, epidermal cells of lamina, and elongated epidermal cells of petiole.

length of nearly a meter, bearing branches or buds at distances of 3 to 8 cm., the distance from the bulb to the first and lower branch being slightly in excess of that of the normal. In some places, however, the intervals were so short that three or four branches were crowded on a portion of stem not more than a centimeter in length. In some instances the buds developed branches 6 to 8 mm. long, subtended by small bracts of equal length. A bract about 7 cm. long, perfectly white, was formed at the base of each stem, being about double the normal length.[131]

A comparison with the normal shows that an excessive elongation has taken place in the basal portion of the shoot, and that the development of the terminal portion has been hindered and the growth of the branches almost totally suppressed. The plant is normally a twiner, clinging closely and firmly to supports, but the etiolated specimens were unresponsive to the presence of vertical supports and were held to it by means of cords. The terminal portions of the stems exhibited an apogeotropic reaction.

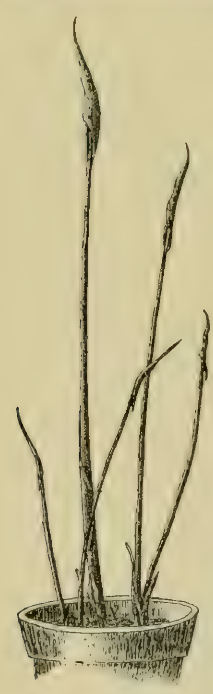

Fig. 40. Etiolated culture of *Arodes*.

The thickening of the outer walls of the epidermis was notably less in the etiolated examples. Stomata were present, and were open when examined in water. The layer of parenchymatous tissue beneath the epidermis, which usually contains many chloroplasts and starch granules in the normal plant was almost free from plastids and solid bodies of all kinds in the etiolated examples. The sclerenchyma ring internal to the cortical tissue is but slightly thickened, and the fibro vascular tissues show but little development.

Brassica campestris L.

Large turnips were placed in the dark room in February and the leaves were soon sent out, growing very rapidly and attaining full size by the end of March. The shoots reached a total height of 55 cm. Leaves attained a length of 13 cm., of which 4–6 cm. lay in the petioles. The narrow laminae were pale yellow and endured less than a fortnight, the entire shoot perishing very quickly. The epidermis both of the laminae and of the petioles showed excessive elongation, and also perfect and open stomata, in addition to large numbers of these organs which did not reach the stage of full differentiation of the guard cells. The fleshy roots perished quickly after the death of the leaves.

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[131] For a general description of the development and growth of *Bowiea* see Buchenau, F., Die Wachstumsverhältnisse von *Bowiea volubilis* Hkr. fil. Abhandl. d. Naturw. Ver. z. Bremen. **6**: 433.

Caladium esculentum Vent.

Corms of *Caladium* placed in the dark chamber in February, 1900, soon began to send up a succession of leaves with petioles 1 to 1.3 meters in length, with the laminae only partly unrolled. These laminae showed an extension of 25 cm. in length and 15 cm. in width when flattened out. The epidermal cells of the laminae were very nearly the same as the normal in general size and outline, but those of the petiole were excessively elongated in a degree fairly correspondent with the petiole. The production of the etiolated leaves continued without interruption for a period of about 20 months, when the main bud perished, and activity of the lateral buds was exhibited in the same manner for some time.

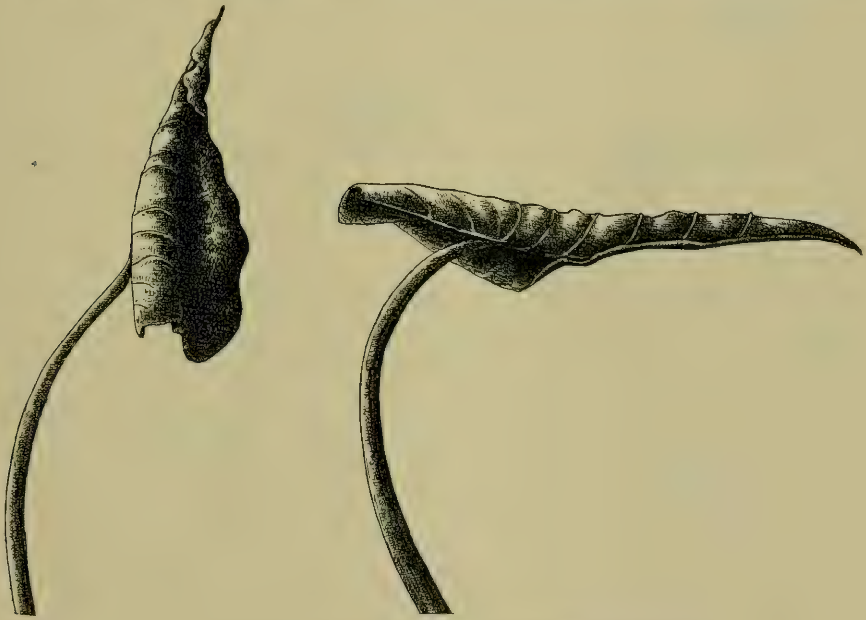

FIG. 41. Etiolated leaves of *Caladium esculentum*.

It is to be seen that *Caladium* is capable of making a sustained effort to carry its chlorophyl surfaces up to light by means of the comparatively enormous amount of energy stored up in its large corms. A second series of cultures gave approximately similar results, and the behavior of this plant is much like that of Arodes, to which it is closely similar in form and development.

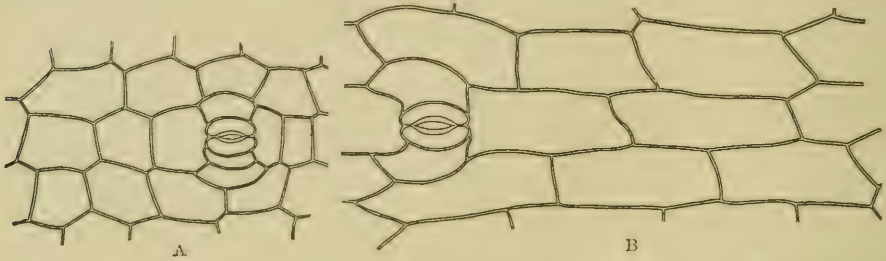

FIG. 42. Epidermis of petioles of *Caladium esculentum*. *A*, normal. *B*, etiolated.

Calla (cultivated).

Large corms of *Arodes* (*Calla Aethiopica*) placed in the dark chamber in November developed two large leaves and a flower stalk within a month. The flower did not reach the advanced stages of *Arisaema*, and the spathe remained tightly wrapped about the spadix. The leaves quickly died down, and a succession of these organs was formed continuously with no apparent resting period for nearly a year, when, the corm being nearly exhausted, death ensued. The leaves showed some chlorophyl under the conditions in which most of the species examined were entirely blanched, except the ferns (Fig. 40).

The following comparative analyses of the aërial organs were made;

ETIOLATED LAMINAE AND PETIOLE.

Weight of fresh material	5.520
" " dried "	.399
" " ash,	.027
Percentage of water	92.77
" " dried matter	7.23
" " ash in fresh material	.049
" " " " dried "	6.76

NORMAL LAMINA AND PETIOLE.

Weight of fresh material	4.290
" " dried "	.440
" " ash,	.031

Percentage of water	89.73
“ “ dried matter	10.27
“ “ ash in fresh material	.72
“ “ “ “ dried “	7.04

Calla palustris L.

Rootstocks of *Calla palustris* were taken in a resting stage in April, and placed in dishes of water and mud in the dark chamber in April. The plant is a native of bogs and often grows in the mud at the bottom of shallow pools. Etiolated leaves had laminae slightly less than the normal, while the petioles was somewhat elongated beyond the normal. No other differences of importance could be discovered.

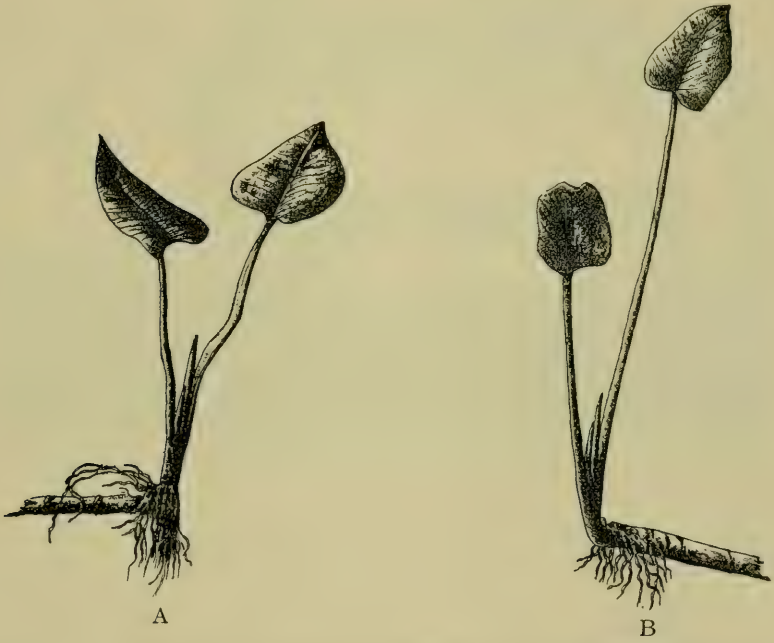

Fig. 43. *A*, normal example of *Calla palustris*. *B*, etiolated example of *Calla palustris*.

Camassia sp.

Bulbs of a *Quamasia* (*Camassia*) placed in the dark room in midwinter soon began a slow growth, the bud pushing up to a length of 2 cm. before opening. The sheathing scale had a length of about 3 cm.

and the leaves developed to the normal length. The inflorescence remained in the form of a slender bud with a scape about 3 cm. long.

The outer leaf was attached to a precision auxanometer in such manner that the nutations of the tip were prevented and a complete continuous record for the entire period of growth was obtained, during a period of about fifty days. A study of this curve fails to reveal any regular rhythmic action. Elongation varied from the average rate above and below it at times, but such fluctuations were doubtless due in part to the application of water to the cultures which was done at various times of the day, whenever necessary. The temperature was constant to within 3° C. as described above. (See Fig. 45.)

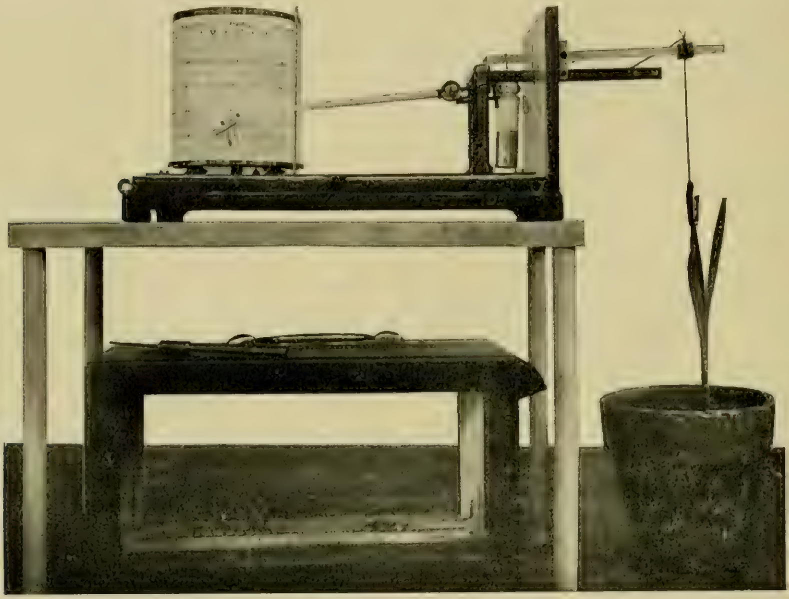

FIG. 44. Precision auxanometer used in measuring growth of leaf of *Quamasia* The instrument is shown with the lever attached to a leaf of *Hyacinthus*, and is adjusted to magnify the elongation forty-five times. (For full description of construction and use see MacDougal's Practical Text Book of Plant Physiology, pp. 291, 292. 1901.)

Canna (cultivated).

Rootstocks of *Canna* placed in the dark room soon began to send up a succession of leaves, which reached a maximum length of 45 cm. and which had a lamina more attenuated than the normal, being about 40 cm. long, and only 8 cm. in width. Such alterations from

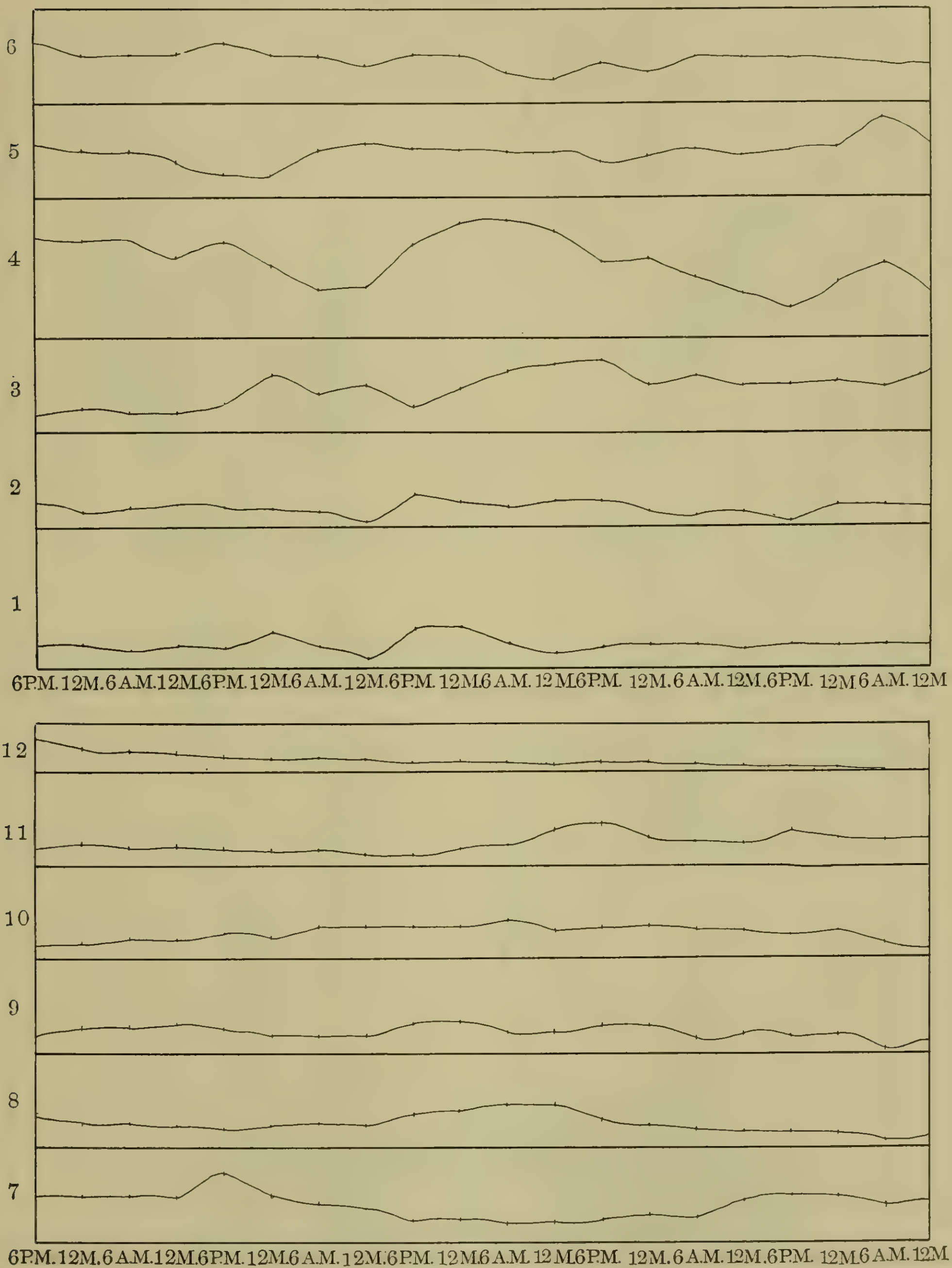

FIG. 45. Curve of growth of leaf of *Quamasia*. Plotted from data obtained by precision auxanometer.

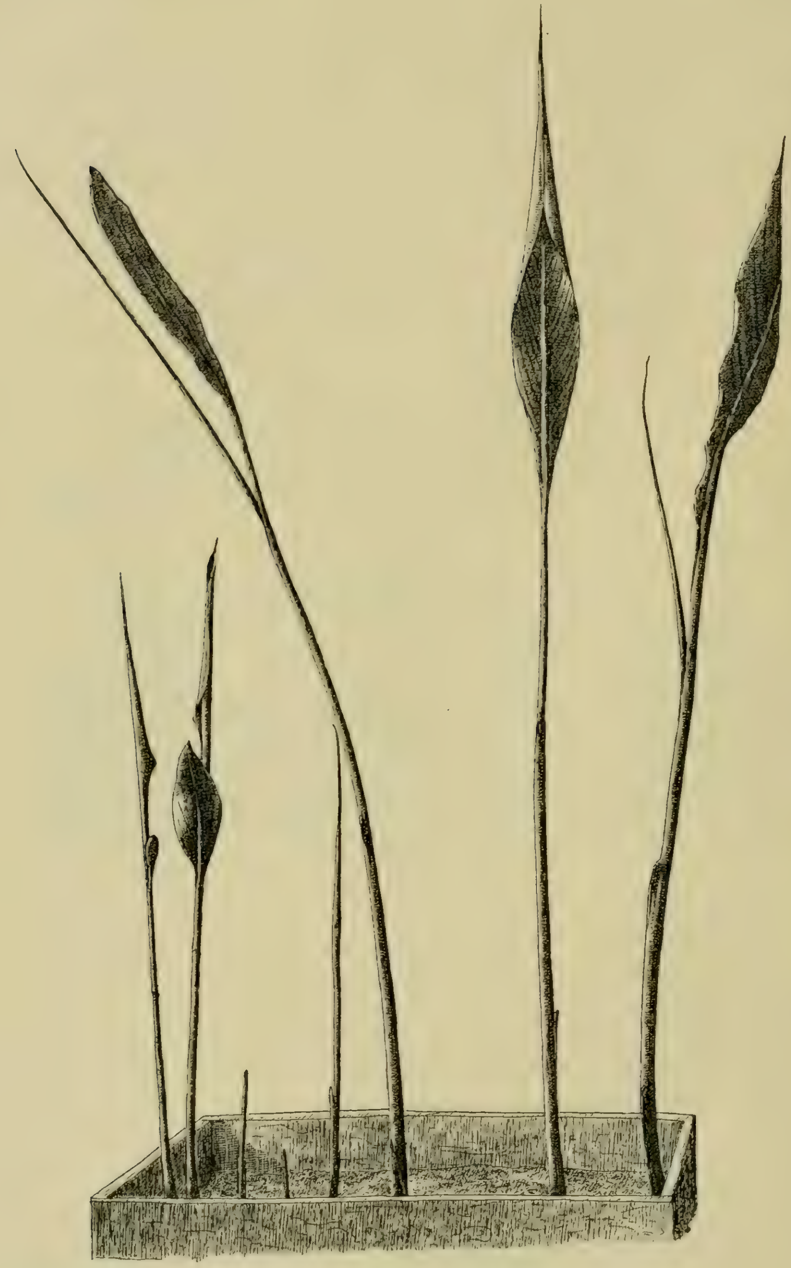

FIG. 46. Etiolated culture of *Canna*.

the normal were accompanied by excessive growth of the epidermal cells, and by the formation of stomata apparently normal, and open when examined in water. Guttation from the margins and apex of the etiolated leaves was very marked. After four or five months' continuous leaf production the rootstocks perished.

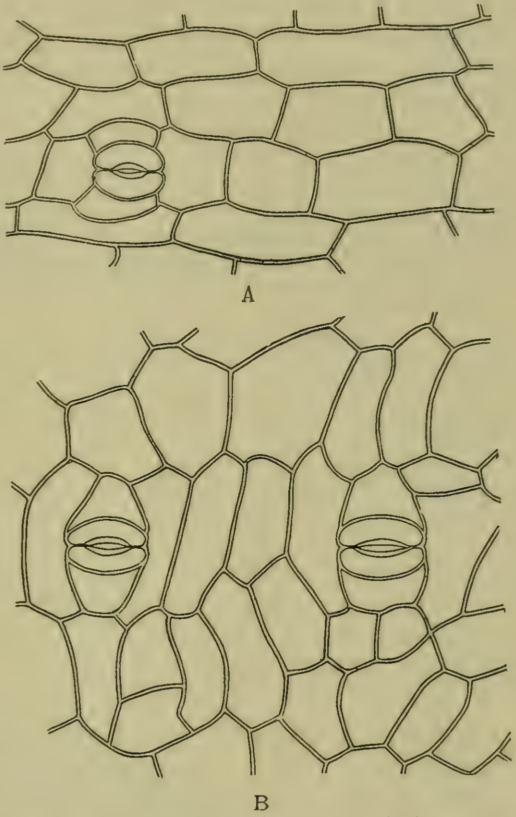

FIG. 47. Epidermis of laminae of *Canna*. *A*, normal. *B*, etiolated.

Castanea dentata (Marsh) Borkh.

A number of chestnuts were placed in moist soil in the dark room and control house October 10, 1901, and began germination about fifty days later. The stems had reached a length of 10 to 12 cm. on January 1, 1902. After a length of 25 cm. had been reached the terminal buds perished, and branches from the first or second bud below took up active growth, sending up stems which had reached a length of 15 cm. by April 4, 1902. (See Fig. 48.)

The basal portion of the shoot below the point of insertion of the cotyledons showed a diameter of 6 mm. and the main stem about half that amount. The entire main stem and the basal portion of the branch in the illustrated specimen had assumed a brownish hue in consequence of the changes in the cortex and epidermis replacing the normal formation of bark. The leaves were all bract-like and showed two stipular appendages of nearly equal size, all of much the same character as those borne on the first three normal internodes. It is quite significant that this etiolated seedling showed nothing but the earlier reduced and primitive leaf forms, and about the same number of internodes as the normal seedling.

Normal seedlings comparable to the above were of a height of about 25 cm. above the point of insertion of the cotyledons. The basal portion of the stem had a thickness of 3 mm. and the shoot above the cotyledons had a diameter of 2 mm. and tapered gradually toward the apex by reason of the greater amount of secondary thickening in the older regions. The formation of bark was well advanced and numerous lenticels were present. The normal seedlings were furnished with three leaves of approximate adult form and size on the terminal portion of the stem, while on the internodes immediately below were four leaves of a length not greater than one sixth of the adult with the dentation indistinct or entirely lacking.

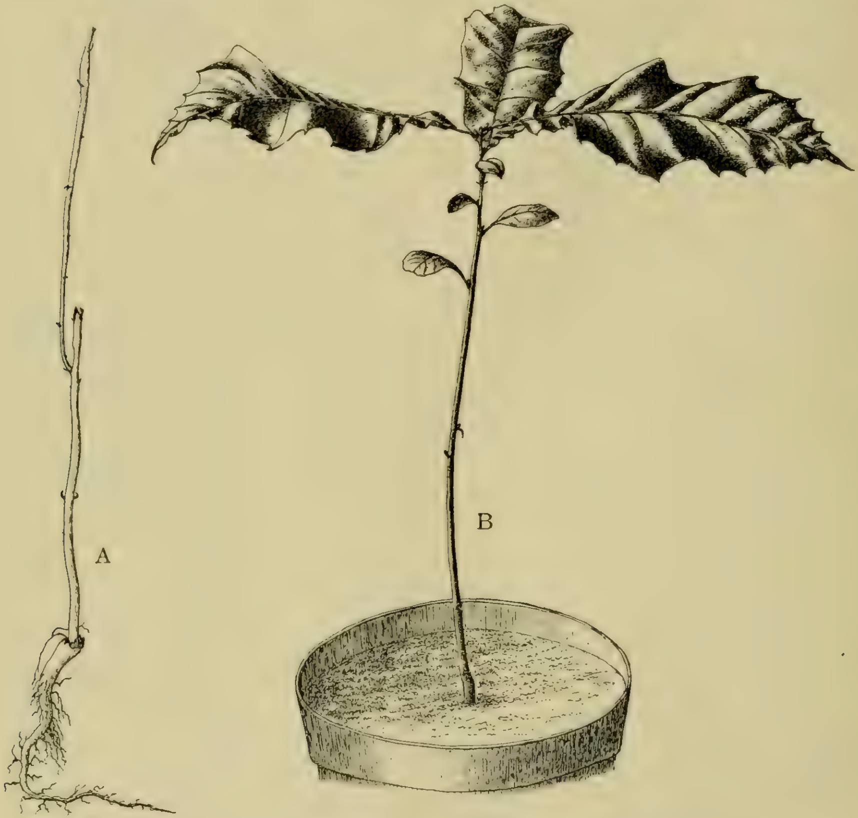

FIG. 48. *Castanea dentata.* *A*, etiolated. *B*, normal plantlet.

The terminal portion of the etiolated stem showed a ring of protoxylem with an indistinct cambium region, which shaded gradually into the bast fibers external to it. The bast fibers were distinguishable chiefly by their position, the walls being but little heavier than those of the cortical cells. The thick layer of cortex was composed of elements, the radial diameter of which was greater than that of the tangential. The epidermis was composed of elements with walls but little heavier than those of the cortex. One or two subepidermal layers of the latter were slightly thickened, however. A few stomatal organs with widely open apertures were found, which would represent the beginning stage of lenticels. The cross section of the lower portion of the etiolated stem above the point of insertion of the cotyledons showed an increase of the pith, the formation of a thin wood ring, and the absence of secondary tissues. The cambium layer had taken on distinctness in places, and a layer of phellogen was visible in the medio-cortex. The bast fiber cells showed about half the normal thickening.

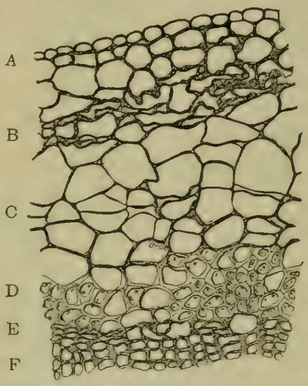

FIG. 49. Partial cross-section of etiolated stem of *Castanea*. *A*, epidermis. *B*, collapsing layer in cortex. *C*, phellogen. *D*, hard bast. *E*, cambium. *F*, wood.

The normal stem shows an outer layer of phellogen bounded internally by a cylinder of collenchymatous tissue immediately internal to which the cortical cells contain chlorophyl.

A region of cortical cells shows the same indications of collapse as in the etiolated stem, but the formation of a dividing layer in the medio-cortex is not present in the normal stem.

Cicuta maculata L.

Clusters of dormant roots were brought into the dark room in the first week in February, 1901, and the stems began growth within a few days, reaching maturity in about four weeks. The stems developed four or five compressed internodes, from each of which a single leaf arose. The leaves were held nearly erect and the petioles were two or three times as long as the normal. The branches of the petiole in the hypopodial region were only slightly and irregularly developed, the laminar tissues remaining in very rudimentary form in closely rolled clumps. The leaves soon perished, and growth ceased. The rootstocks remained alive however and might have been capable of another effort under proper cultural conditions.

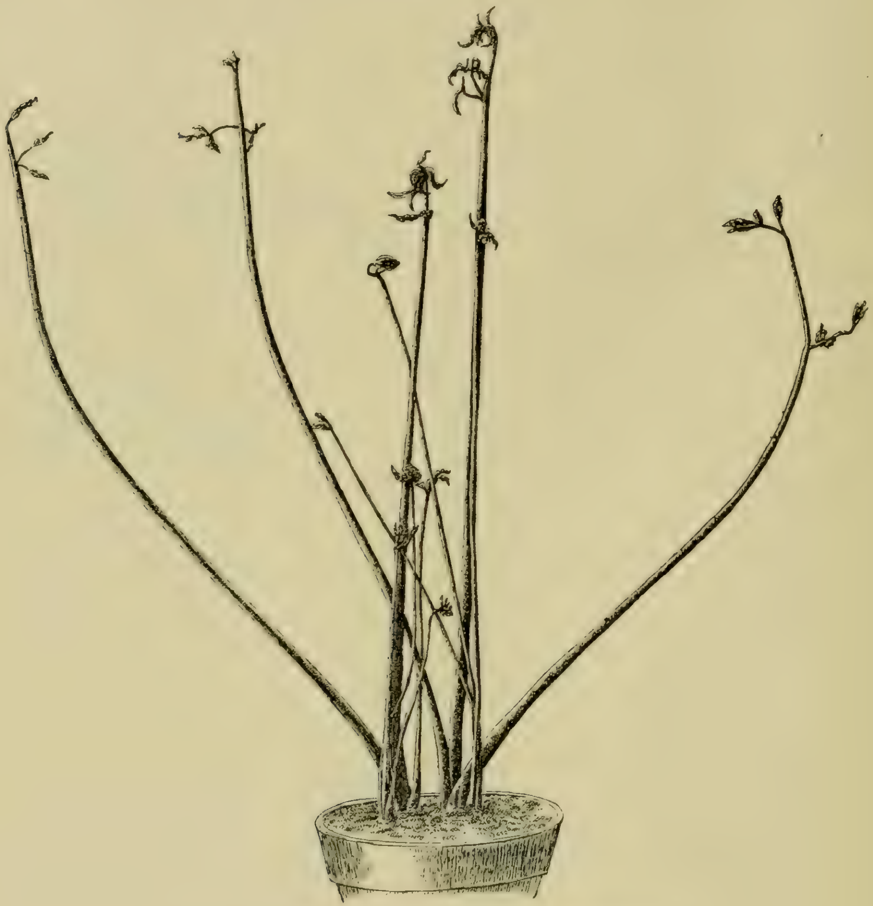

FIG. 50. Etiolated cultures of *Cicuta maculata.*

The above reactions were practically duplicated in tests with *Thaspium trifoliatum* grown in small dark chambers at the University of Minnesota in 1898 and 1899, and all umbelliferous species behave in this manner so far as my observations extend.

Claytonia Virginica L.

Tubers of *Claytonia* placed in the dark room in April, at a time when natural growth of the buds was taking place, did not show more than a third of the normal size of the stems, although the tubers still contained a comparatively enormous amount of reserve food. The flower buds remained unopened and the leaves perished quickly. It is quite probable that the limited action shown by this species was due to the temperature, which was much higher than that encountered in the open air during its period of blooming. The plant would need the capacity of elongation to free itself from the layers of leaves which accumulate to some depth in its habitats.

Cocos nucifera L.[132]

A number of cocoanuts in the husk, freshly arrived from Jamaica, placed in moist soil in December, 1899, soon germinated, and were placed in the dark room in February, 1900. Leaves were formed from the plantlets which differed from the normal chiefly in a slight

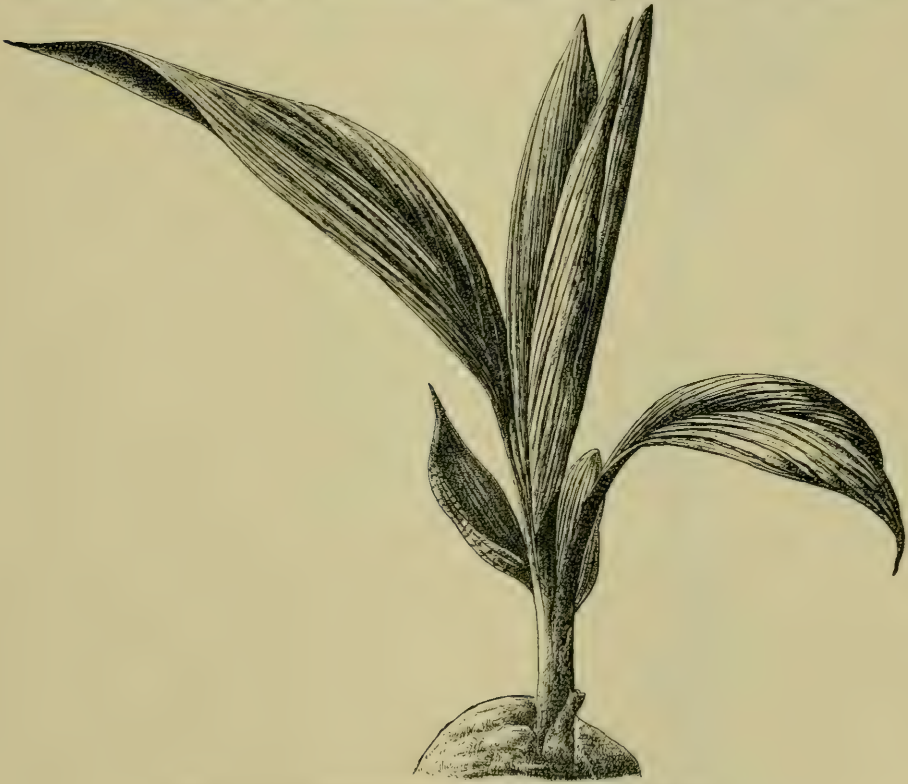

FIG. 51. *Cocos nucifera.* Shoot of normal plantlet.

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[132] See Kirkwood and Gies. Chemical Studies of the Cocoanut and its Changes During Germination. Bull. Torr. Club **29**: 321–359. 1902.

attenuation of the broad laminar portion. A year later, after continuous growth in the interval, the fourth pair of leaves had arrived at maturity in the darkness. A specimen examined on March 6 had absorbed all of the endosperm from the apical end of the fruit, but a great amount of food was still present as a layer increasing in thickness toward the opposite end, where it had been decreased but slightly from its original thickness. The absorbing organ completely filled the central cavity, and its rough rugose outer coat was closely pressed against the remaining layer of endosperm. A neck or cylindrical body a centimeter in thickness connected the absorbing organ with the young plantlet. The roots were furnished with numerous lenticels. Numerous stomata, open when examined in water, were found on the leaves in the epidermis of the lower side. The upper, inner, side of the leaf seemed to be free from transpiring organs of any kind. Chlorophyl was developed very quickly under the influence of illumination of a gas jet of six candle power at a distance of three meters.

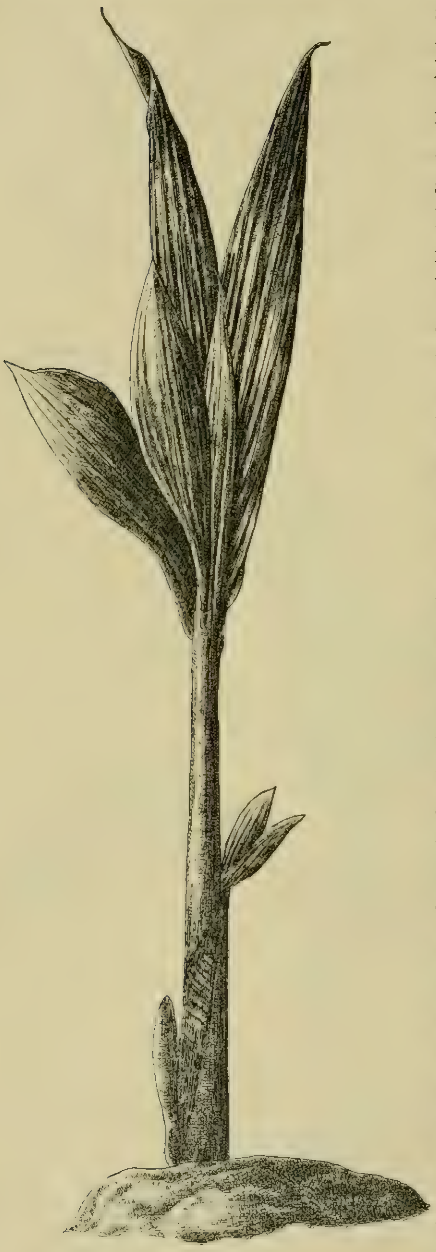


FIG. 52. *Cocos nucifera.* Etiolated shoot of plantlet after 15 months' confinement ni dark room.

A second specimen examined on May 22, 1901, had developed the sixth pair of leaves, a sparse root system, the main root being about 3 cm. in diameter at base, and had not used more than half of the food stored in the endosperm, during the period of 15 months in which it had lived saprophytically on the stored food in the fruit. During my absence in the summer of 1901 all of the specimens perished. In this as well as in other seedlings the power of extended existence by means of the food stored in the seed is seen.

Coix Lachryma-Jobi L.

Seeds of *Coix* placed in the soil in November, 1899, germinated in the following March and at the end of April had attained a height of 25 cm., showing one basal leaf unfolded, and another still in the rolled form. The internodes were about 5 cm. long with sheathing petioles of the same length. The blades had a length of 8–10 cm., and were a centimeter wide at the greatest extension.

Normal control examples were 15 cm. in height and the sheathing bases of the leaves about 3.5 cm. in length. The blades were 1.2 cm. wide and 8 cm. long. The lowest internode was about 5 cm. in length, and the one above it 1 cm. It is thus to be seen that the stems are excessively elongated and the leaves also, the latter being but little narrower than the normal.

Colocasia sp.

Corms of a cultivated *Colocasia* were placed in the dark room, in February, 1900, and developed leaves with petioles a meter or more in length, with the laminae only partly unrolled and held in a horizontal position, after the usual habit of the caladiums. The laminae attained a length of 10–20 cm. Second and third leaves were produced in quick succession and then the corms were allowed to go into a condition of rest through the summer. Upon the application of water to the cultures in September, 1900, the formation of leaves recommenced. The slight exposures to light in the examinations with a paraffine candle were sufficient to induce the construction of chlorophyl, in this as well as in caladiums and cultivated callas. (See page 86.) The leaves were found to be proheliotropic to such feeble illuminations, and apogeotropic. Guttation was very marked, the exudations issuing from the apices, margins and injured portions of the leaves.

Cornus alternifolia L. f.

Vigorous shrubs of *Cornus* 3 meters in height were taken from the soil about December 1, 1901, and after a period in a cool chamber were placed in the control and dark chambers in the middle of December. The first activity was observed in the specimens placed in the dark chamber on January 18, 1902, at which time a number of buds midway on the branches and on the middle portion of the stem began to elongate. Later all buds on the main axis and branches in the upper portion of the shoot perished and only those from the basal portion survived. These, however, showed a vigorous growth. It was found that the upper part of the stems of all of the plants had died as a result of the transplanting. It is noteworthy that the awakening buds were all infra-axillary. On April 6 some of the young etiolated branches had attained a length of 18–20 cm., at which time a photograph was taken from which the accompanying drawing was made. A few branches measured twice this length on June 17, 1902.

The etiolated branches assumed an attitude very nearly vertical, in consequence of which some of them were appressed to the stem. No branching occurred except in one or two instances. In such the uppermost pair as well as the terminal bud would elongate approximately equally. The leaves on etiolated branches attained a length of nearly a centimeter, but remained small and bract-like, although giving some imitation of the adult form. The hairs so noticeable in the young normal stems and leaves were present even on the older portions of etiolated stems and were very abundant on the younger portions. These hairs consisted of a short upright stalk bearing a slender ovoid capitate cell with its long axis parallel to the surface. The branches retained their colorless aspect for some time, and showed a slight tinge of brown in June, five months after their appearance.

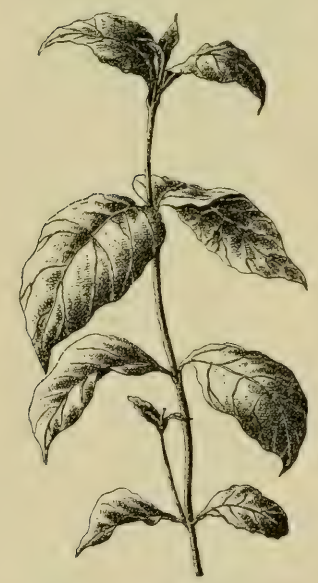


FIG. 53. *Cornus alternifolia*. Normal branch.

The cross-section of the apical internode of the etiolated stem showed the pith in the process of enlargement, a thin cylinder of wood cells with an indistinct cambium layer. The bast fibers formed an incomplete circle of spindle-form cells with but little thickening. The cortex was composed of the customary thin-walled cells, which with the pith contained some starch, and was furnished with intercellular spaces. The epidermal cells were slightly thickened as also one or two layers of hypodermal tissue. Some widely open stomata were present.

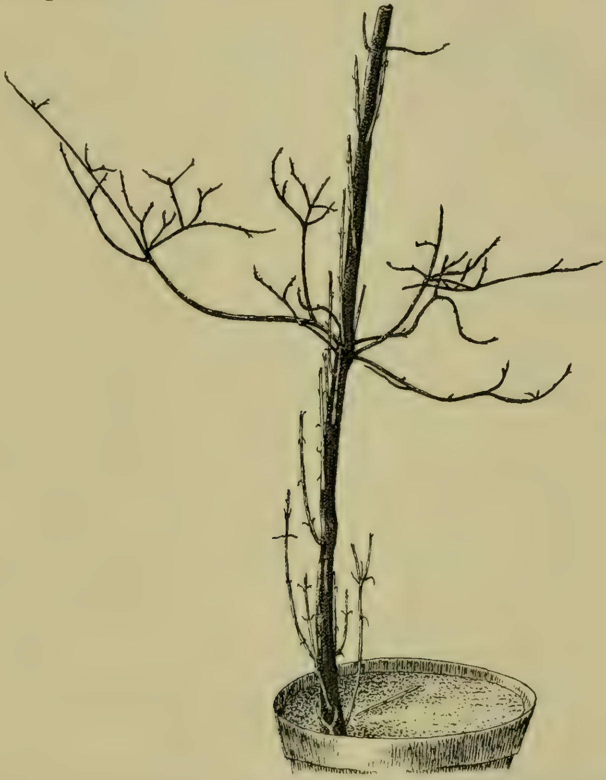


FIG. 54. *Cornus alternifolia.* Base of young tree with spreading normal branches and upright etiolated branches.

In the older internodes the pith had attained twice the original diameter, the wood ring had increased by continuous and uniform external additions, and some thickening had ensued in the bast fibers. The number of these elements had not increased, and the walls were pushed inwardly in some instances as if the cells had collapsed. No indications of collapse were to be seen in the outer layers of cortex, or in any way comparable to that seen in *Castanea*, a fact which is correlated with the shorter period of duration of *Cornus*. The formation of a distinct phellogen in the epidermal region had reached an advanced stage, and was followed by some discoloration of the epidermis.

Normal stems of the same age showed no indications of the formation of phellogen. The cortical cells were smaller than in the etiolated with the tangential greater than the radial diameter. The bast cells were much like those of the etiolated stem. A region immediately underneath the epidermis contained much chlorophyl, which also extended down into the pith through the rays. No marked differences in the trichomes could be found.

Cyclamen sp.

Corms of *Cyclamen* purchased from a dealer were placed in moist soil in the dark room in January, 1900. The growth of the leaves soon began, and elongated petioles were formed, which were soon

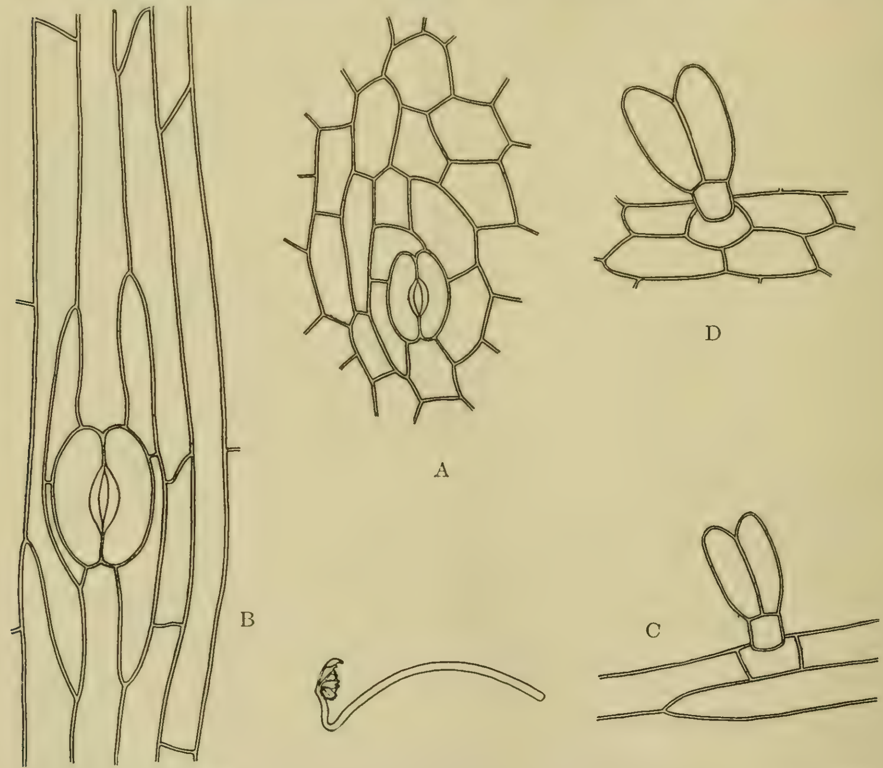


FIG. 55. *Cyclamen*. *A*, normal epidermis. *B*, etiolated epidermis. *C*, etiolated hairs, from the petiole. *D*, normal hairs from petiole. Terminal portion of petiole with etiolated lamina.

prostrate with the apical, terminal portion apogeotropic, and bearing the small undeveloped laminae with the upper (inner) surfaces appressed. The petioles and laminae were purplish in color, and the epidermis bore short hairs filled with a reddish cell sap. The etiolated hairs were slightly smaller than the normal. The epidermal cells were excessively elongated, being four or five times as long as the normal, and the stomata were larger and apparently functional.

The production of leaves continued more or less irregularly during a period of 18 months, and then the activity slowed down, and the corms went into a state of rest from which it was impossible to rouse them, although still sound and healthy. In no instance were the flower stalks developed.

Cypripedium montanum Dougl.

Dormant specimens of *Cypripedium* were placed in the dark chamber in January, 1900, and began growth a month later. Two months later a young flower bud was pushed out from among the etiolated leaves, but did not open or attain normal size.

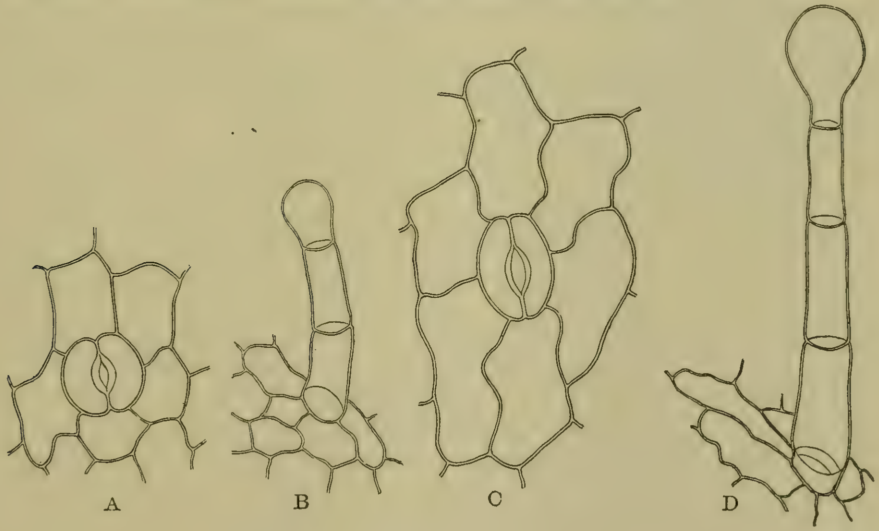


FIG. 56. *A*, epidermis from normal leaf of *Cypripedium montanum*. *B*, glandular hair from surface of normal leaf. *C*, epidermis of etiolated leaf. *D*, glandular hair from etiolated leaf.

The main stem attained a length of only 2 cm., which is only a fraction of that of the normal. The excessively elongated leaves were 15 cm. in length, and 2.5 cm. wide, while the normal leaves are 8 by 3.2 cm.

Epidermal cells from the lower surfaces of the etiolated leaves measured 32 by 4 while those of the normal were only 15 by 10. Etiolated leaves bore glandular hairs only, the pointed trichomes being absent. The shaft of the glandular hairs in the normal, consists of two cells with an average total length of 50 and diameter of 4, while in the etiolated the shaft was composed of four cells of an average total length of 110 with a diameter of 12. The apical gland measured 22 by 19.5 in the etiolated, and 16 by 13 in the normal.

From the above facts it is to be seen that the growth of *Cypripedium* in darkness is characterized by a non-development of the pointed hairs on the leaves, and the excessive development of the glandular trichomes. The first result is in accord with Schober's results, but no reason is at hand to account for the excessive enlargement of the glands and the multiplication of the cells in the stalk, unless these organs might be considered as aids to transpiration. The stomata of the leaves were of normal size, but of slightly attenuated outline, being apparently functionally normal.

The laminae maintained an erect position, and were more or less rolled during all of the period of their existence, embracing about a month.

Delphinium exaltatum Ait.

A number of rootstocks of *Delphinium exaltatum* were potted and brought into the dark room on January 18, 1900, and began to grow at once. The main stem attained a length of 8 cm. as against the normal of 4 cm. and the total height was 28 cm. while normal plants under similar conditions were only 15 cm. high. The etiolated petioles reached a length of 10 to 30 cm. while the normal measured only 4 to 6, thus showing the most excessive elongations in the petioles. The petioles assumed a negatively geotropic position with the laminae pendent by means of a curvature at the extreme tip of the petiole. The actual rate of growth was about twice that of the normal, during a period of ten days kept under observation.

An etiolated specimen was cut off and the base of the shoot thrust into water in a calibrated measure, through a cork which was smeared with vaseline to prevent evaporation from the water surface. The total volume of the exposed stem was 5 c.c. and included 6 etiolated leaves. 1 c.c. of water was taken up in 24 hours in the dark room at a temperature of 16–18° C. A shoot of a normal plant with seven leaves, the whole having a volume of 2 c.c. used 2 c.c., or its own volume of water in 24 hours at a temperature of 18 to 20° C. in diffuse daylight. (See Fig. 57.)

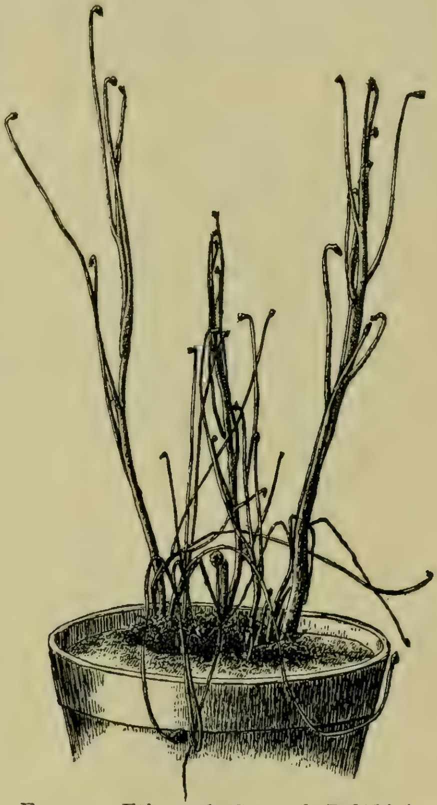


Fig. 57. Etiotated shoot of *Delphinium exaltatum*.

Equisetum arvense L.

A number of bulb-bearing underground stems of *Eqisetum arvense* were placed in a dark room in January, 1900, and a month later two sporophytes and a number of vegetative shoots were to be seen. The latter developed only a small number of branches to a length equal and greater than the normal, the remainder attaining a length of a centimeter or two, and the whole shoot showed some attenuation. In only two instances out of 40 under observation did these branches give rise to branches of the second order. The vegetative shoots perished within sixty days, which may have been due to defective cultural conditions. (See Fig. 58.)

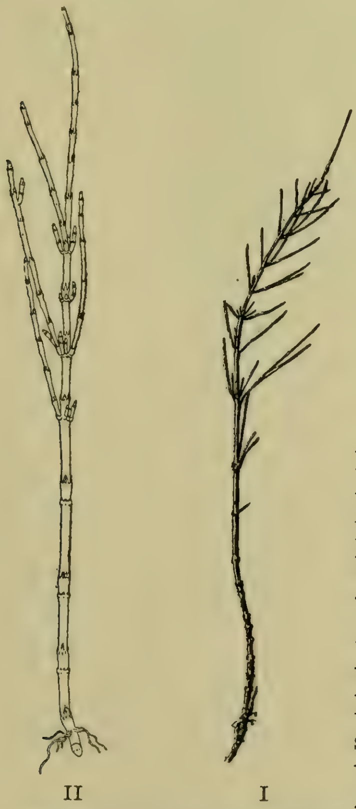


Fig. 58. I, normal young vegetative shoot of *Equisetum arvense*. II, etiolated shoot.

A few spore-bearing stalks or sporophytes developed to a height of a few centimeters, and the spores appeared fairly normal in structure, showing a green coloring matter, but the sporangia did not open and the spores soon perished.

Erythronium Hartwegi S. Wats.

Numbers of bulbs of *Erythronium Hartwegi* obtained from dealers were placed in the dark chamber in the spring of 1901, and a single leaf 12 to 15 cm. long was sent up from every one. The leaf, as well as most of the bulbs, soon perished, however, probably due to imperfect cultural conditions.

Falcata comosa (L.) Kuntze.

Tubers of *Falcata comosa* were placed in the dark chamber in the spring of 1899, and rapidly developed stems. A comparison with control examples showed that the lowest internode of the normal stem was 7 cm. in length and that a runner was sent out from this internode which grew to the length of a meter or more, while in the etiolated examples the lowest internode attained a length of 13 to 28 cm., and the runners were represented by branches not more than a centimeter in length.

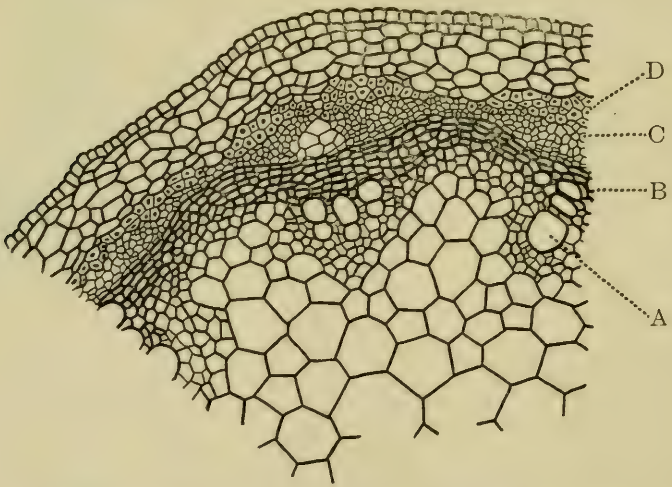


FIG. 59. Partial cross section of normal stem of *Falcata*. *A*, xylem. *B*, sclerenchyma. *C*, sieve tissue. *D*, bast fibers. × 80.

The successive internodes in the normal measured 3, 3, 4, and 5 cm., while in the etiolated all of the internodes above the basal one described above, had a length of 7 and 8 cm. It is thus to be seen that etiolation phenomena are shown by this, as well as by all of the other vines examined in the course of the experiments. Furthermore it was found that in no instance did these vines exhibit a tendency to twine about supports as in the normal.

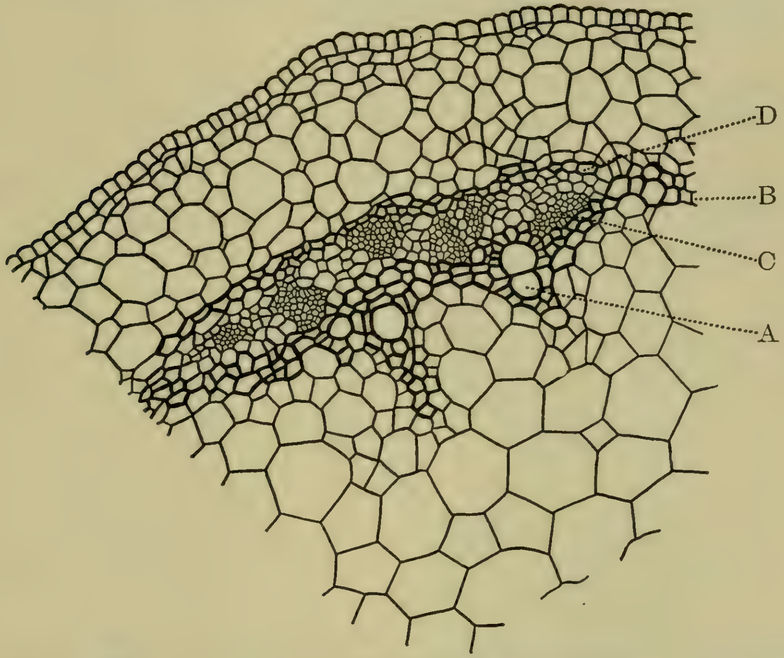


FIG. 60. Partial cross section of etiolated stem of *Falcata comosa*. × 80. Description as in Fig. 60.

The leaves remained as very small rudiments. Etiolated stems were thicker than the normal by reason of the excessive development of the cortex and pith. The epidermal cells of etiolated plants were larger than the normal in all dimensions. The sclerenchyma showed less thickening, as also the bast fibers, and less sieve tissue was differentiated than in the normal. The xylem was also less developed than in the normal.

Fagus Americana Sweet.

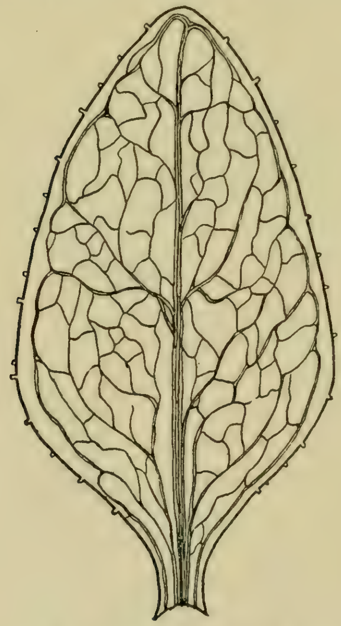
Trees of *Fagus Americana* 3 meters in height were placed in the control house about December 1, 1901, having been taken from the soil and placed in large pots. About half of the buds were removed from all of the plants. A young plant 25 cm. in height which had been in the greenhouse three years was also placed in the dark chamber. No action of any kind was shown as late as June 23d although the temperature was probably suitable for this species. Similar results were obtained by Jost with *Fagus*. (See p. 26.)

Filix fragilis (L.) Underw.

Rhizomes taken from the soil at New Canaan, Conn., on November 28, 1900, soon showed activity and developed fronds with midribs 25 cm. long with 5 pairs of pinnae. The pinnules were unfolded, being about 4 cm. long. The lower pairs were opposite in the usual manner, but the upper pinnules were variously alternated. The entire frond was deeply tinged with chlorophyl. The rootstocks were intact after this growth, and could doubtless send up other fronds after a resting season.

Galium circaezans Michx.

Rootstocks of *Galium circaezans* placed in the dark room in January, 1900, developed stems which were 30 cm. long with the ongest internode measuring 7 cm. on March 22. The leaves were partially rolled on the long axis, ovate, and with an obtuse apex.



IG. 61. Normal leaf of *Galium circaezans*.

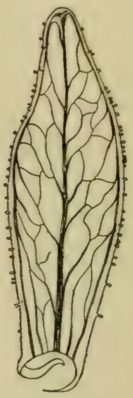


FIG. 62. Etiolated leaf of *Galium circaezans*.

The middle nerve only was apparent. Motile stomata were present which were open when examined in water. The stems were about 2 mm. in diameter and were circular in cross section, the angles of the normal stem being entirely lacking. Glandular hairs and functional stomata were also present. The epidermis was composed of cells of rounded outlines in cross section, and the collenchyma usually present in the angles was entirely absent. The etiolated cortex was extremely thin-walled, and showed intercellular spaces. The stele remained in an embryonic condition. The vessels of the xylem and protoxylem were barely distinguishable, and groups of sieve tissue might be seen. The epidermal cells of the etiolated stem were scarcely more elongated than the normal, but are wider in surface view. The angle of the stem in the normal bears a duct furnished with glands of the usual stature. The stomata were closely crowded together as if the entire number had been formed in the earlier states of development and were not separated by the normal development of the epidermis, which did not take place. Anthocyan was present in the leaf, and masses of a yellowish substance in the parenchyma cells of the laminae, and also in the etiolated shoot. The epi-

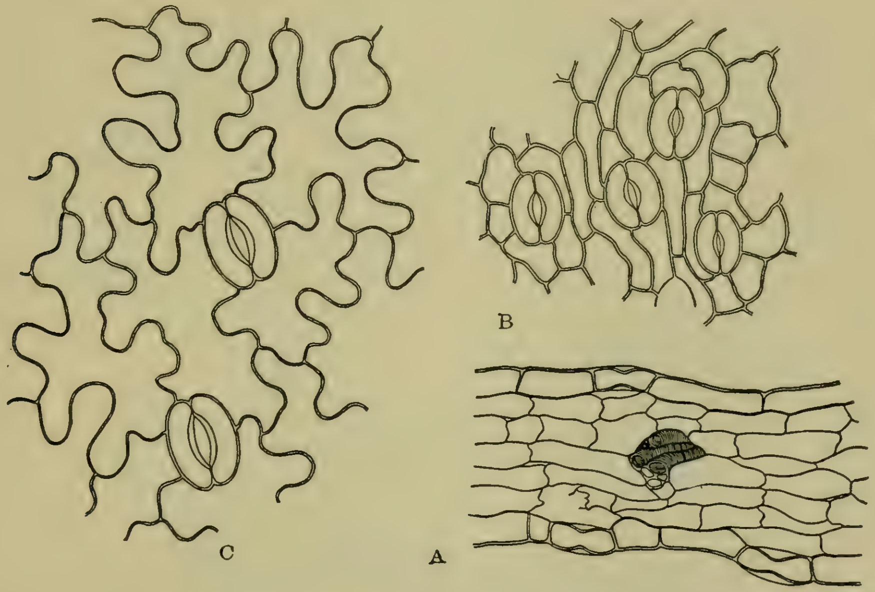


FIG. 63. *Galium circaezans*. *A*, transverse section of etiolated lamina. *B*, epidermis of etiolated leaf. *C*, epidermis of normal leaf.

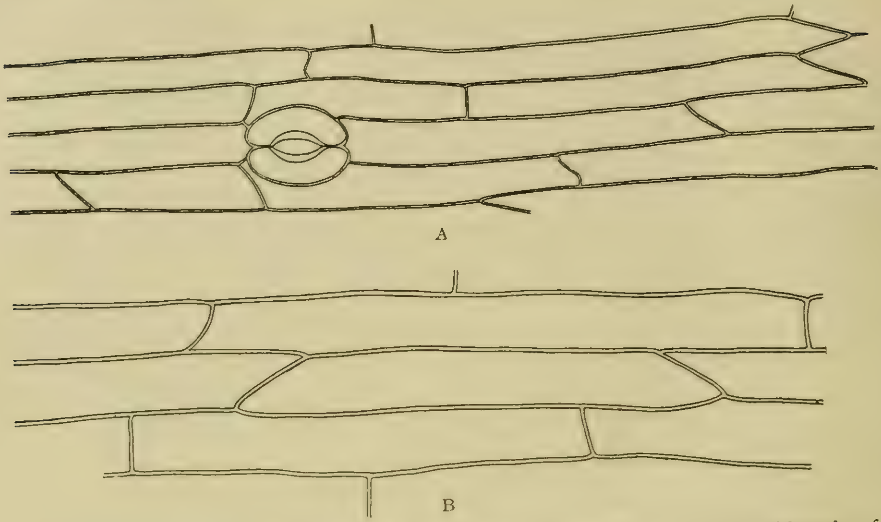


FIG. 64. *Galium circaezans.* *A*, epidermis of normal stem. *B*, epidermis of etiolated stem. × 20.

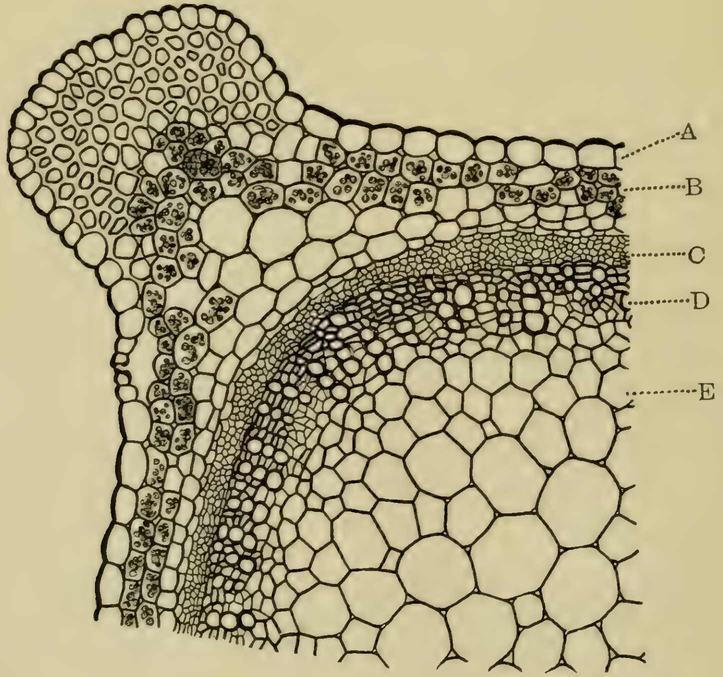


FIG. 65. Partial cross section of normal stem of *Galium circaezans.* *A*, epidermis. *B*, cortex containing chlorophyl. *C*, sieve tissue. *D*, xylem. *E*, pith.

dermal cells of the leaf were naturally smaller in the etiolated organs and more regular in outline, while the palisade tissue, and spongy parenchyma are not differentiated.

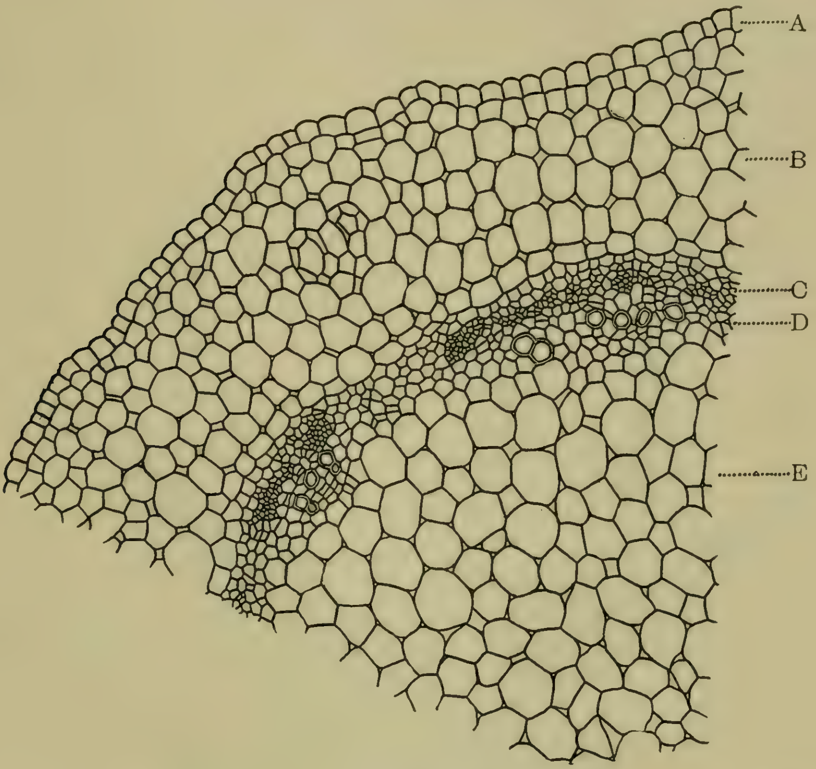


FIG. 66. Partial cross section of etiolated stem of *Galium circaezans*. Description same as in Fig. 65, except that the cortex contains no chlorophyl.

Gasteria disticha Haw.

A single specimen brought into the dark room in September, 1900, soon began growth. The young leaves, the apices of which were barely exposed, were carried into an erect position instead of being brought to the horizontal as in the normal. A small offset with thin linear or lanceolate leaves was developed from the basal internode, reaching a length of several centimeters on May 20. (See Fig. 67.) This branch perished during the summer. Similar elongation, and erection of propagative branches was to be noted in *Sanseveria*. The main stem was greatly elongated, the internodes attaining a length of 3 or 4 cm. and were partly exposed instead of being entirely sheathed by the leaf bases as in the normal. A single slender inflorescence axis was developed from the axis of the first leaf reaching a length of 4 cm. and then underwent atrophy. The normal leaf of this species is roughly rectangular in cross-section, while the etiolated was double convex. The rugose formations of the normal leaf were lacking in the etiolated, except at the margins of the lower etiolated leaves; those found later were entirely smooth. Etiolated leaves were only half the length of the normal, a fourth of their width, and a third or fourth of their thickness. The chlorophyl of the older leaves was retained with no apparent alteration, and a slight tinge of green was noticeable in etiolated leaves due to the occasional exposure to the light used for inspection.

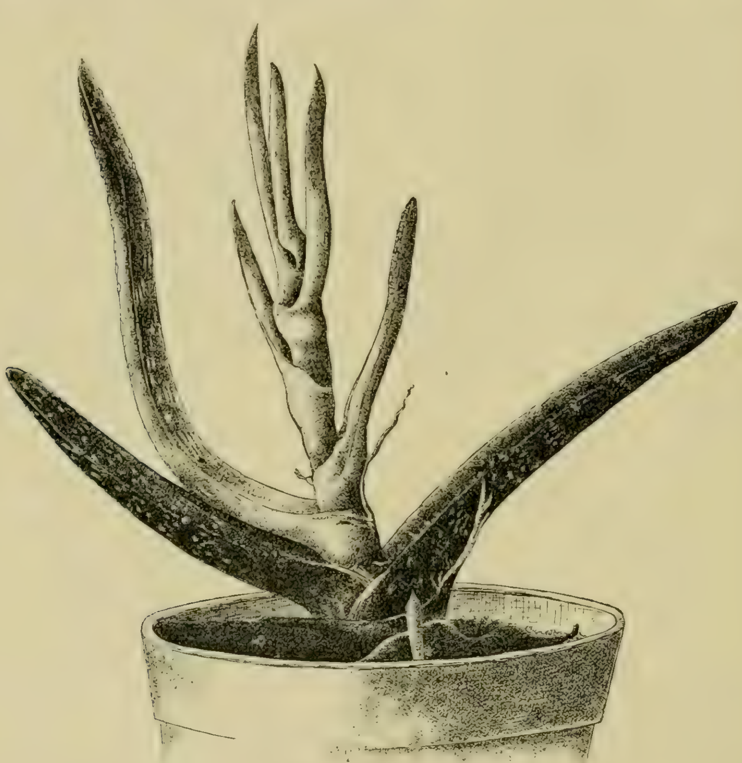


FIG. 67. *Gasteria disticha.* *A*, plant after six months in dark chamber, showing two leaves formed in light, and two partially developed in light which completed their growth in darkness, also inflorescence, stalks and small runner or offset.

Fifteen months after the culture began, the leaves, which had reached full development before confinement in darkness, had perished and the leaves formed partially in light and partially in darkness had begun to die at the tips. (See Fig. 69.) The upper internodes showed a successive increase in the length of the internodes, and the leaves were held at various irregular angles. Such positions were partly due to the rupture of the stems near the nodes and also to the sheathing leaf-bases.

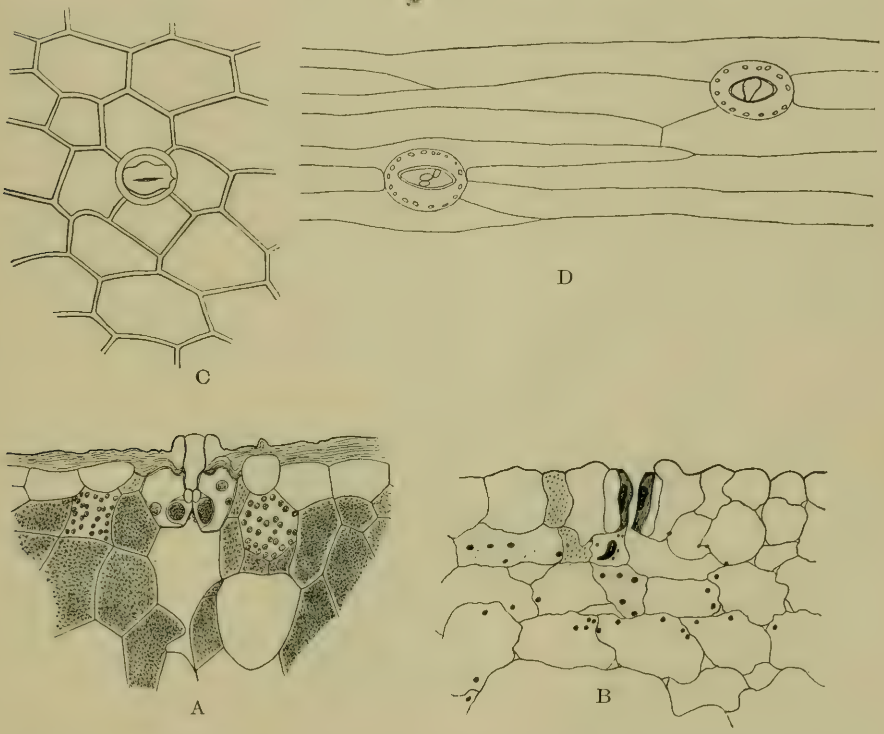


FIG. 68. *Gasteria disticha*. *A*, partial transverse section of normal leaf. *B*, partial transverse section of etiolated leaf. *C*, surface view of normal epidermis of leaf. *D*, surface view of etiolated epidermis.

The structural alterations in etiolated leaves were very marked. The epidermal cells of the normal leaf were irregular polygons in surface view, in which but little difference might be seen in the various diameters. These cells underwent great axial elongation in etiolated organs, and the outer cutinized layer was notably lacking. The guard cells of the normal stomata are extended outwardly making an elevation on the surface of the leaf by a single thickening of the outer cutinized layer. Such thickening was wholly lacking in the etiolated leaf, and the guard cells are slightly sunken below the surface. The guard cells do not undego full differentiation, and the supporting cells were smaller than in the normal, being functionally active however, as attested by the long endurance of the etiolated leaves. The parenchyma cells of the normal leaf are richly loaded with starch and chlorophyl, which were entirely lacking in the etiolated organs, the plastids present being much smaller than the normal.

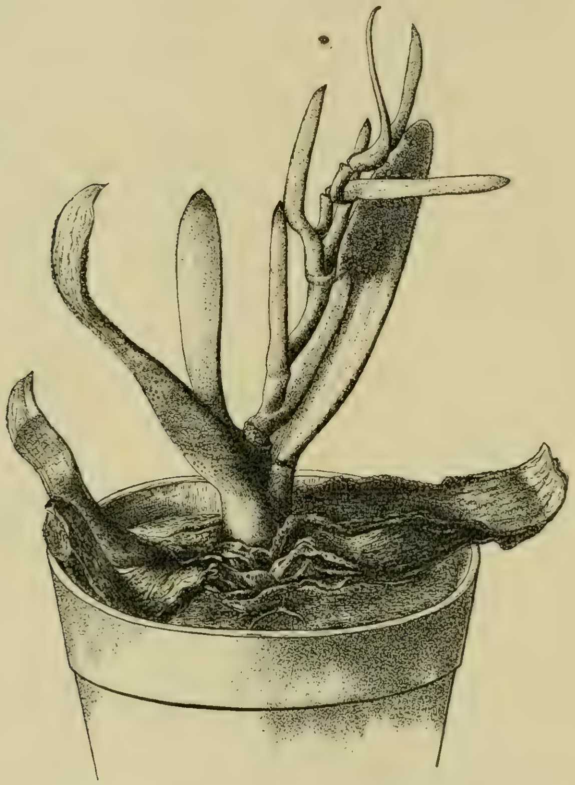


FIG. 69. *Gasteria disticha*. Same plant as in Fig. 67, 14 months after confinement in dark room. The leaves formed in light have perished and the younger etiolated leaves are held in various aberrant positions due to ruptures in the stem.

The growth of the etiolated specimen continued until February, 1902, at which time it was damaged in handling and perished.

Gleditsia triacanthos L.

Seeds placed in a dark chamber in October, 1900, did not germinate until March, after which growth proceeded very slowly. The cotyledons were carried aloft attaining a total length of 15 mm., and were ovate with an auriculate base. The upper, inner surfaces were closely appressed. The cotyledons endured for about 60 days in the dark chamber, when they were thrown off, and the first node of the stem attained a length of 8 mm. bearing a pair of appressed leaves, which did not unfold, but in which the pinnae were distinctly visible. The hypocotyledonary stem attained a length of 18 cm., which is about one and a half times the length of the normal. The root system formed in the dark was very sparse, being made up of a tap root with a very few branches. The lower surfaces of the cotyledons were furnished with stomata, the guard cells of which were loaded with starch, and which were closed when examined in water, being apparently not functional. The seedling perished after the above development had been accomplished.

Hemerocallis sp.

Bulbs of *Hemerocallis* placed in the dark room in early spring after activity had begun in the open, showed an active development which resulted in the formation of leaves 11.5 cm. long. The upper or inner surfaces remained closelya ppressed, and the entire leaf was colored a pale yellow. The flower stalks or inflorescence gave no indications of activity.

Hicoria sp.

A number of nuts from an unknown species of hickory were placed in moist soil in March, 1900, and germinated in May of the same year. The stems had reached a height of 40 cm. to 60 cm. in June and were then checked by the high summer temperature, the terminal buds being destroyed. In November of the same year a renewed growth ensued after the summer resting period, and one more of the original lot of nuts germinated. The apical buds of the older plants being dead the lateral buds nearest awoke, and the branches formed from them assumed the upright positions of the main stems. Some etiolated specimens removed to the illuminated room developed leaves resembling the customary forms in normal cultures. Growth and development of the shoots continued until March, 1901, thus showing that the seedlings were capable of an existence of nearly a year in darkness at the expense of the food stored in the nut.

Hicoria minima (Marsh) Britton.

Nuts of *Hicoria minima* were placed in moist soil in the control chamber, and dark room on October 16, 1901. Three of those in the dark room had germinated and sent up shoots, one of which had reached a length of 12 cm. on January 4, 1902. None of those in the control chamber in illumination had shown activity at this time. On April 16 five plants were to be seen in the illuminated chamber with stems 5 to 8 cm. in length and bearing a number of reduced bract-like leaves and two, trifoliate, or simple laminae. At this time the etiolated specimens had attained a length of 25 cm., in some instances bearing a single straight upright stem with the terminal bud still active. The leaves were simple and bract-like, soon falling off. The lower third of the stem had begun to show a dark brown color

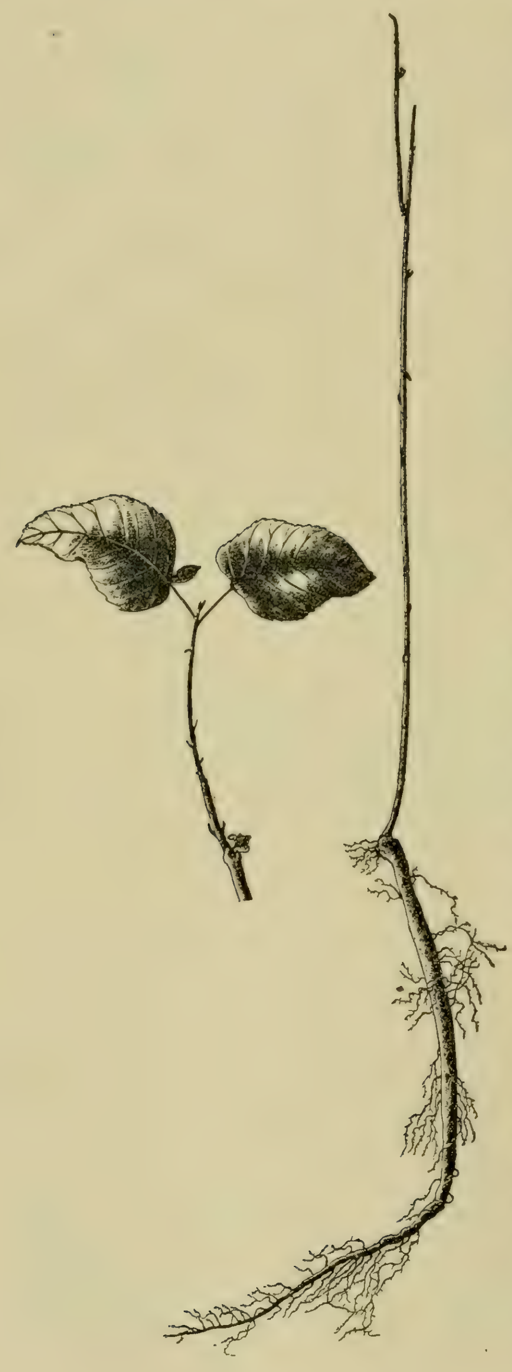


FIG. 70. *Hicoria mimima*. Etiolated shoot and terminal portion of normal shoot

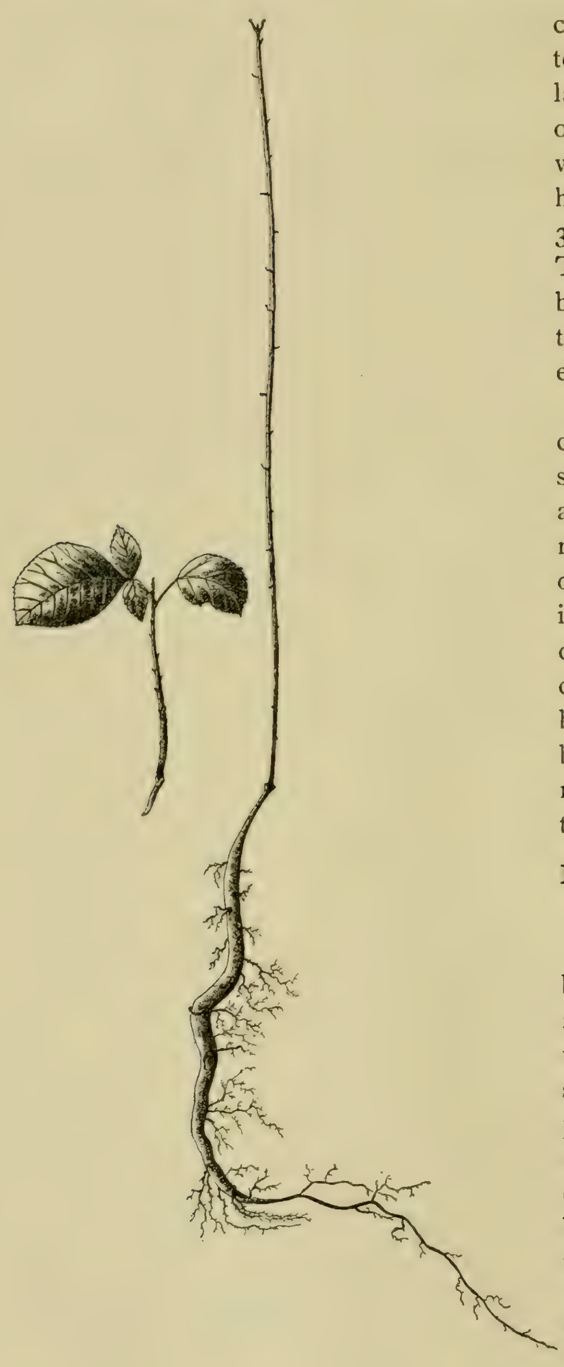
indicative of the earlier, or initial stages of formation of periderm. On June 17 one stem had attained a height of 36 cm. the longest internode measuring 8 cm.

The normal stems of the age of the etiolated showed a brown color at the base due to the death of the epidermal cells. Five or six layers of cork had been formed underneath, and the thick-walled cortex contained much chlorophyl, especially in the outer layers. Crystals were numerously distributed throughout this tissue. A heavy cambium layer was present, and the incomplete ring of bast consisted of cells which had undergone extreme thickening. All of the parenchymatous cells were heavily loaded with starch.

A cross section of the basal portion of the etiolated stem that had begun to turn brown showed the epidermal system in a fairly normal condition with the walls white and translucent. The usual formation of cork in the hypodermal region was lacking, but a median region in the cortex had begun to collapse, the walls assuming a brownish hue giving the external color to the stem. The entire cortical region had thinner walls than in the normal and both starch and crystals were noticeably less abundant than in the normal. In this as well as in *Cornus* and *Quercus*, the lack of cork formation in the hypodermal region was accompanied by the development of a phellogen immediately external to the cylinder of bast cells, sometimes in immediate contact with the collapsed layer: the bast fibers were nearly normal in stature so far as might be seen in cross section. A distinct layer of primary cambium could not always be made out, and the walls of the wood cells were not so heavy as in the normal. The above collapse of the median region of the cortex was accompanied, or followed, by the shrinkage of the basal portion of the stem in such a manner that it had a smaller diameter than the terminal portion, a phenomenon also seen in *Quercus*.

Hicoria ovata (Mill) Britton.

Nuts of *Hicoria ovata* placed in the soil in the control chamber, and the dark room on October 16, 1901, had begun to germinate on January 4, 1902. On April 16, one young plant with two primitive leaves was seen in the control chamber, the stem being about 8 cm. long above the place of insertion of the cotyledons. The lower part of this stem bore a few bract-like leaves. Two seedlings were found in the dark room. One had sent up a main stem about 25



cm. in height, when the terminal bud perished. A lateral bud then developed an erect branch which extended the total height of the shoot about 30 cm. above the soil. The terminal bud of this branch also perished and the growth of other lateral buds had begun.

The behavior of the cortical and epidermal tissues was much the same as in *H. minima*. The median collapsing layer of cortex turned brownish-yellow, and with the disintegrating epidermal cells gave the stem a brownish-black hue. The bast fibers were fewer in number, and but little thickened in any instance.

Hyacinthus sp. (grape hyacinth).

Leaves of awakening bulbs attained a length of 25 cm. in darkness, which were crescentic in cross section, and yellowish, or perhaps slightly greenish at the tips. The presence of some chlorophyl was to be detected in many plants, the leaves of which were

FIG. 71. *Hicoria ovata*. Etiolated plantlet, and terminal portion of normal shoot.

formed in the buds of the bulbs or corms. The flower buds retained their dormant condition for a time, then perished. The widths of the normal and etiolated leaves were found to be about equal, but the etiolated leaf was a half longer than the normal green one. When etiolated leaves were brought into light no further increase could be detected either in width or length. A slight flattening of the partially rolled or curved leaves ensued, however.

Hyacinthus sp.

Hyacinthus sp. developed leaves 30 cm. in length, which were rolled in tube form, and were 11 and 12 cm. in width when flattened out for measurement. Secondary leaves from lateral scales of the bulb attained half this length and retained the cylindrical form. No development of the inflorescence could be seen.

Hydrastis Canadensis L.

Rootstocks of *Hydrastis Canadensis* placed in the dark room in January began growth a month later. Sterile stalks bearing only leaves reached a height of 30 cm. with a diameter about equal, or in some instances exceeding the normal. The petiole at first showed an elbow immediately below the lamina, but which disappeared on maturity, and the lobes of the lamina were appressed with the upper surfaces together and directed upward. The stems bearing both leaves and flowers showed a much greater elongation, but their length bore about the same proportion to the normal. The curvature of the petiole at first enclosed or shielded the peduncle and pendulous flower bud, thus presenting an elbow of stem as it pushed upward. Finally, however, the petiole became erect, as well as the peduncle which was formerly protected by it.

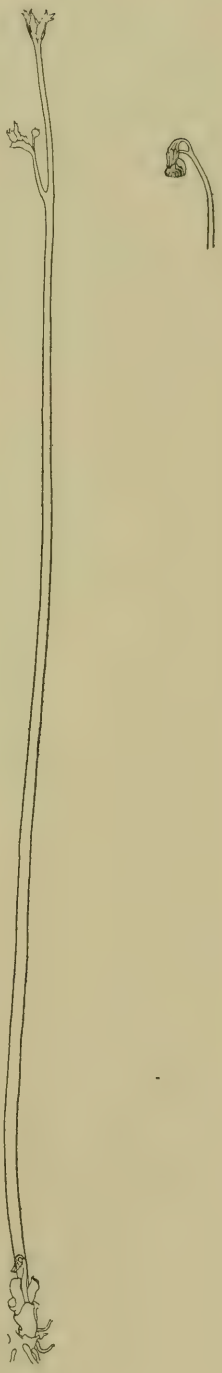


FIG. 72. *Hydrastis*. Etiolated stem.

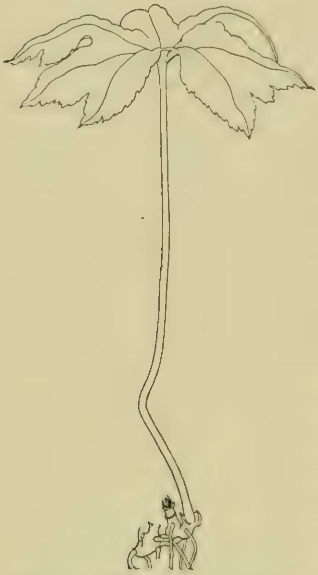


FIG. 73. *Hydrastis.* Normal leaf.

Starch was lacking from the etiolated petioles except in the guard cells of the stomata. The fibrovascular tissues were fairly normal in their general development and structure, and the stems were approximately of the same degree of rigidity as the normal. The epidermal cells of the etiolated stems were slightly elongated. The hairs borne on etiolated stems were not more than one fourth of the length of the normal. Similar differences are to be found on the leaves. The stomata of both the laminae and the stems were slightly open when examined in water and appeared to be functional. No rhythm in growth could be detected from an examination of the auxanometric measurements. (See Fig. 74.)

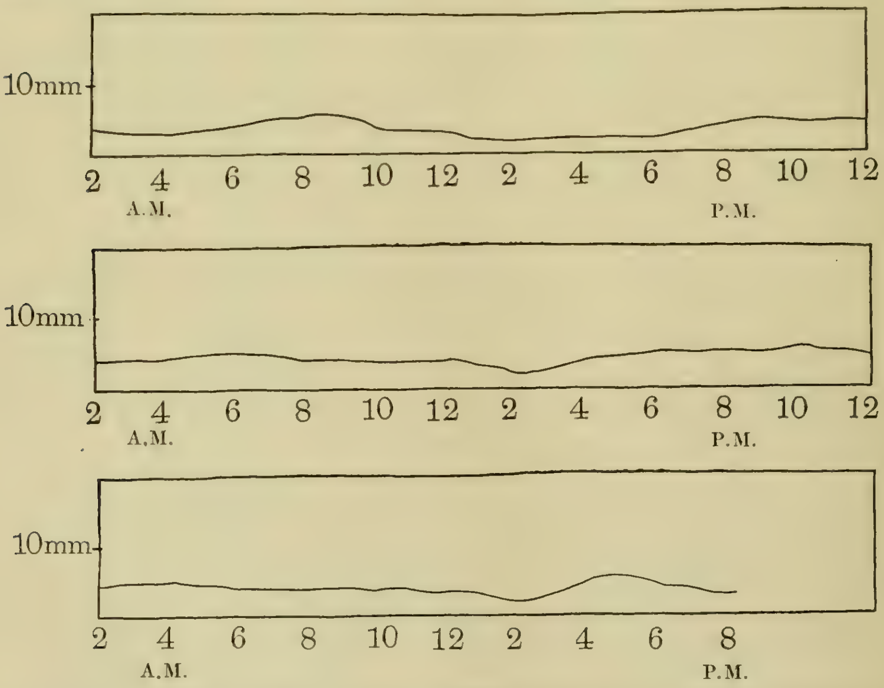


FIG. 74. Curve of growth of stem of *Hydrastis* during three days in dark room at a temperature constant between 22 and 24° C.

Hypopitys Hypopitys (L.) Small.

Clumps of *Hypopitys* which were breaking through the soil near the Marine laboratory at Cold Spring Harbor, Long Island, in 1899 were covered in such manner as to exclude light. No appreciable difference in the stature or appearance of these plants and others in the light could be detected. This test was repeated at Woods Holl, Mass., in the same year, and also at Priest River, Idaho, in the following year with the same result. It is also notable that this plant does not usually exhibit phototropic curvatures, although as may be seen by reference to the historical sketch, many fungi are capable of both etiolative and phototropic reactions.

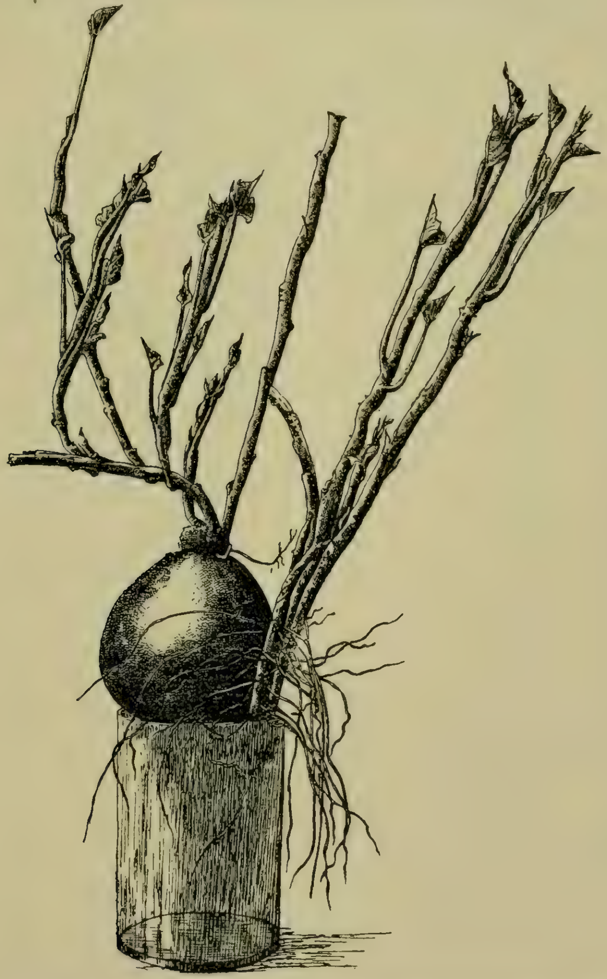


FIG. 75. Etiolated stems arising from tubercle of sweet potato.

Ipomœa Batatas Poir.

Tubercles of the sweet potato placed in moist soil in the dark room in November began to produce stems in January, and sent out a succession of these organs, which were apogeotropic, but soon became decumbent with the terminal portions curved upward. The apical buds soon perished, and the lateral growing points began activity.

The leaves developed petioles a half or two thirds of the normal length, with the laminae folded with the ventral surfaces together. The laminae did not attain a superficial area of more than a tenth of the normal. The leaves were crowded together on the basal portion of the stem, being not more than 1 or 2 cm. apart on a section about 20 cm. long, in normal plants. Above this the leaves are more scattered on a portion of the stem in which twining usually takes place. This terminal twining portion was not developed in the etiolated plants. (See Fig. 75.)

No important differences could be detected between the structure of normal and etiolated stems. The leaves quickly perished and dropped off, leaving a distinct protuberance at the point of connection with the stem. (Fig. 75.)

The tubercles perished after the first etiolated growth, and the plant does not seem adapted to making a second effort in darkness.

Iris sp.

Shortly after rootstocks were placed in the dark room the buds began activity, and a succession of leaves was

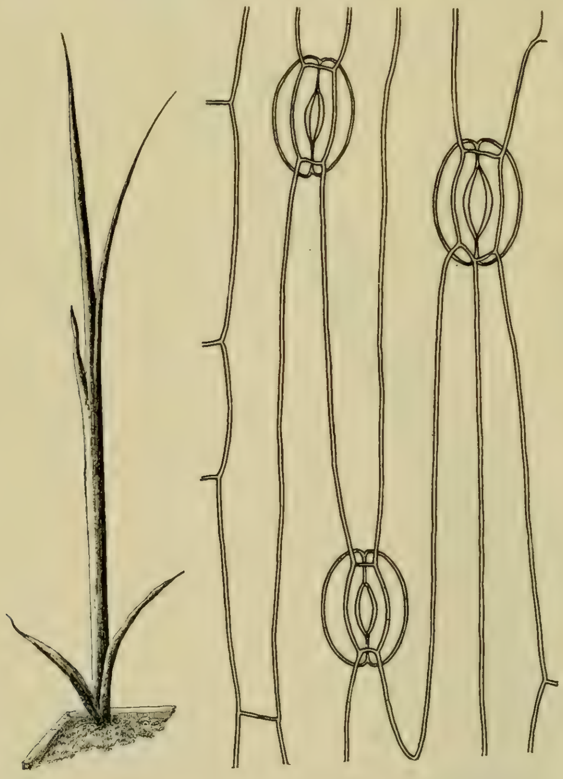
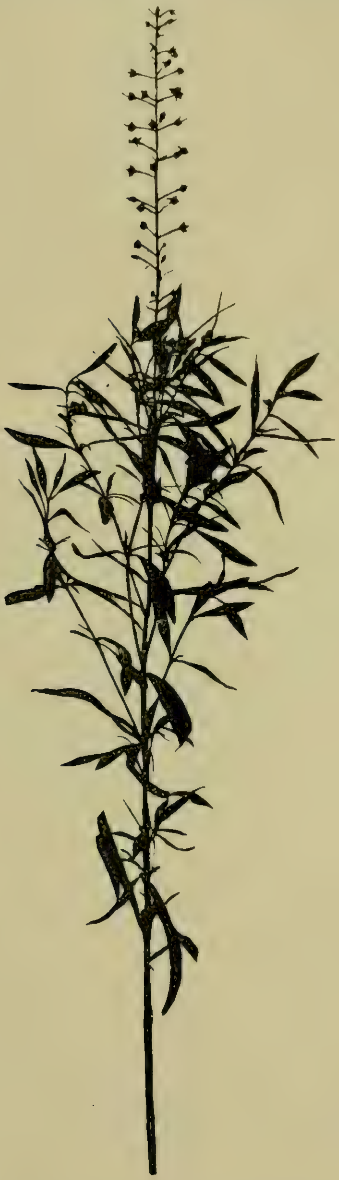


Fig. 76. Etiolated specimen of *Iris*, and epidermis of etiolated leaf.

formed, which were slightly in excess of the normal size. The epidermis was elongated beyond the measurements of the normal, and the leaves did not survive long. The stomata appeared to be functional.



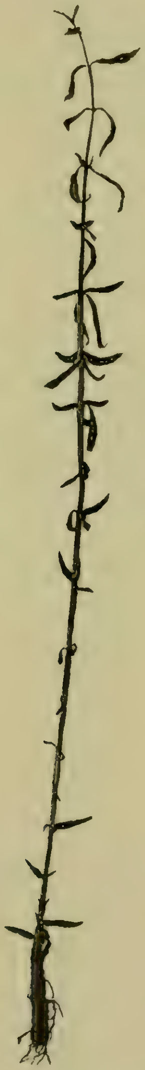


FIG. 77. Normal flowering shoot of *Lysimachia terrestris*, and also shoot grow in diffuse light with branches replaced by bulbils.

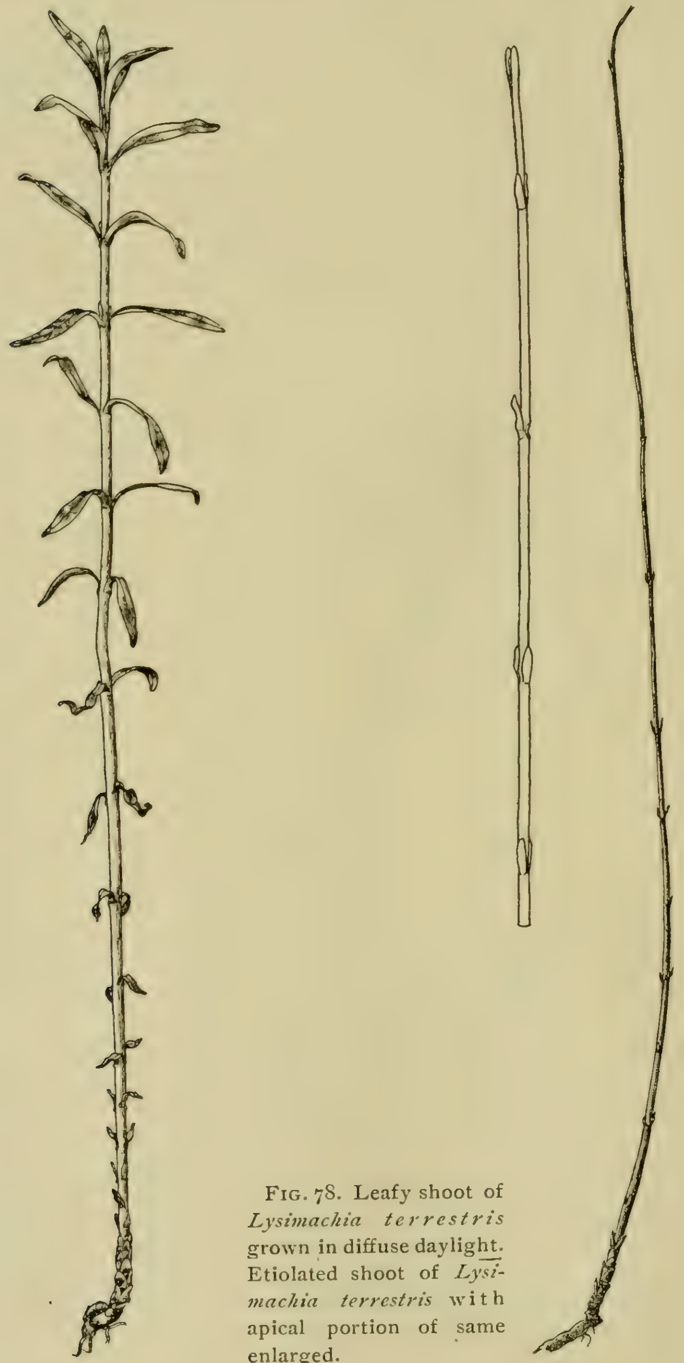


FIG. 78. Leafy shoot of *Lysimachia terrestris* grown in diffuse daylight. Etiolated shoot of *Lysimachia terrestris* with apical portion of same enlarged.

A second series of cultures with a species native to eastern America in March in the dark chamber showed a development of two leaves with a length of 23 and 25 cm. which were free only a few centimeters at the tip. The slightest exposure to the light used in examination was sufficient to stimulate the production of chlorophyl.

Lysimachia terrestris (L.) B.S.P.

Lysimachia terrestris consists of a branching rhizome with aërial leafy stems which may bear flowers, or the numerous branches may be converted into, or remain in the form of, bulbils as the author has discovered in some previous investigations. When such rhizomes are placed in the dark room, slender etiolated stems without branches or bulbils are produced, with internodes of a length of 1 to 5 cm., while in the normal stem the length of the internodes varies from .5 cm. to 3 cm., the longest being found in the middle of the stem below the flower-bearing branches. The total length of the etiolated stem was slightly greater than that of the normal flowering shoot,

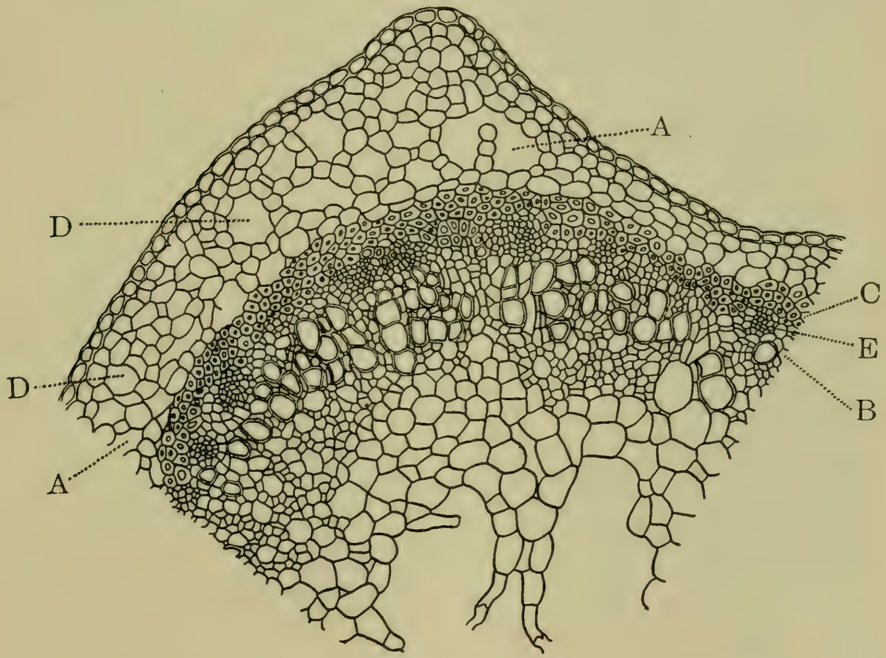


FIG. 79. *Lysimachia terrestris.* Partial transverse section of normal stem. *A*, air-spaces in cortex; *B*, xylem; *C*, bast fibers; *D*, glandular ducts; *E*, sieve tissue.

which continues to elongate during the greater part of its existence in the open. The opposite leaves on the etiolated stems remained in a rudimentary form and were upright, being closely appressed against the stem. The leaves do not attain a length greater than 5 mm. and a width of 1.5 mm., dying away on the lower internodes as the stems progress, much after the same manner as in the normal specimen, so that only three to five pairs were to be seen at one time. The number of internodes in the etiolated and normal stems are practically equal. The diameter of the etiolated stem was barely half that of the normal. The epidermis of the stems as well as of the leaves showed numbers of stalked glands of apparently normal struc-

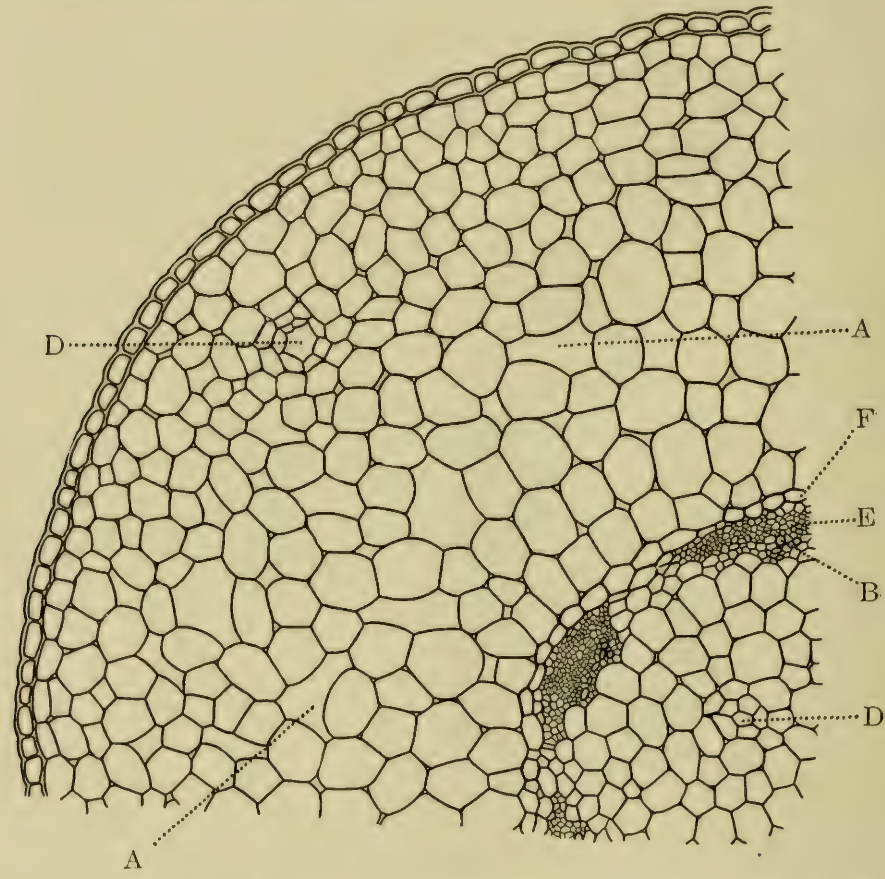


FIG. 80. *Lysimachia terrestris.* Partial transverse section of bulbil. *A*, air spaces; *B*, protoxylem; *E*, protophloëm; *F*, endoderm; *D*, ducts.

ture. The cortical cells of the etiolated stems were richly loaded with starch, as well as the guard cells of the stomata. The difference between the sizes of the epidermal cells in the etiolated and normal specimens was not great. The red anthocyan of the normal specimen was lacking from the etiolated specimen. The great air spaces of the cortex are present in both the etiolated and normal. The glandular ducts were also present. The stele remained in an embryonic condition; the cambium ring was apparent, and was fairly complete. A number of elongated cells in the phloëm with dense contents and strictly transverse walls seemed to be sieve tubes arrested in an early stage of development. A few layers of closely packed parenchyma cells lay closely to the internal surface of the xylem, while the central pith was made up of plates of cells with great air-spaces.

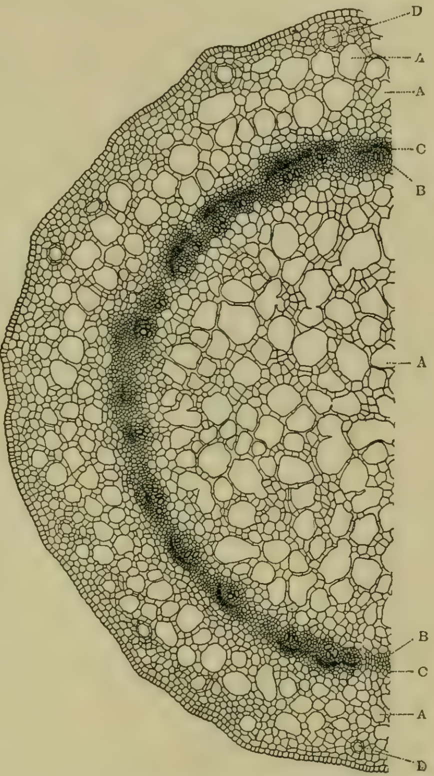


FIG. 81. *Lysimachia terrestris.* Partial transverse section of etiolated stem. *A*, pith and cortex; *BB*, protoxylem; *CC*, sieve-like cells; *DD*, ducts.

A comparison of the etiolated stems, with the bulbils reveals the fact that the anatomy of the two is very closely similar, and both may be regarded as stems in a state of arrested, or very incomplete, differentiation of the tissues.[133]

Menispermum Canadense L.

A number of the underground rhizomes of *Menispermum* were placed in the dark chamber in January, 1900. The aërial stems, which are lateral branches from the rhizomes, soon made their appearance, and in three months attained a length of 25 to 50 cm., with the longest internodes about 5 cm. At this stage the shoots began to perish. The stems seemed to be apogeotropic and exhibited distinct nutating curvatures. The leaves were expanded but extremely small, standing out from the stem at an angle of 50° to 60°, the lower ones perishing before the stems had reached full length. It is to be noted

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[133] MacDougal, D. T. Vegetative propagation of *Lysimachia terrestis.* Bull. N. Y. Botanical Garden, 2: No. 6. p. 82. 1901. See also Practical Text-Book of Plant Physiology, pp. 320, 326. 1901.

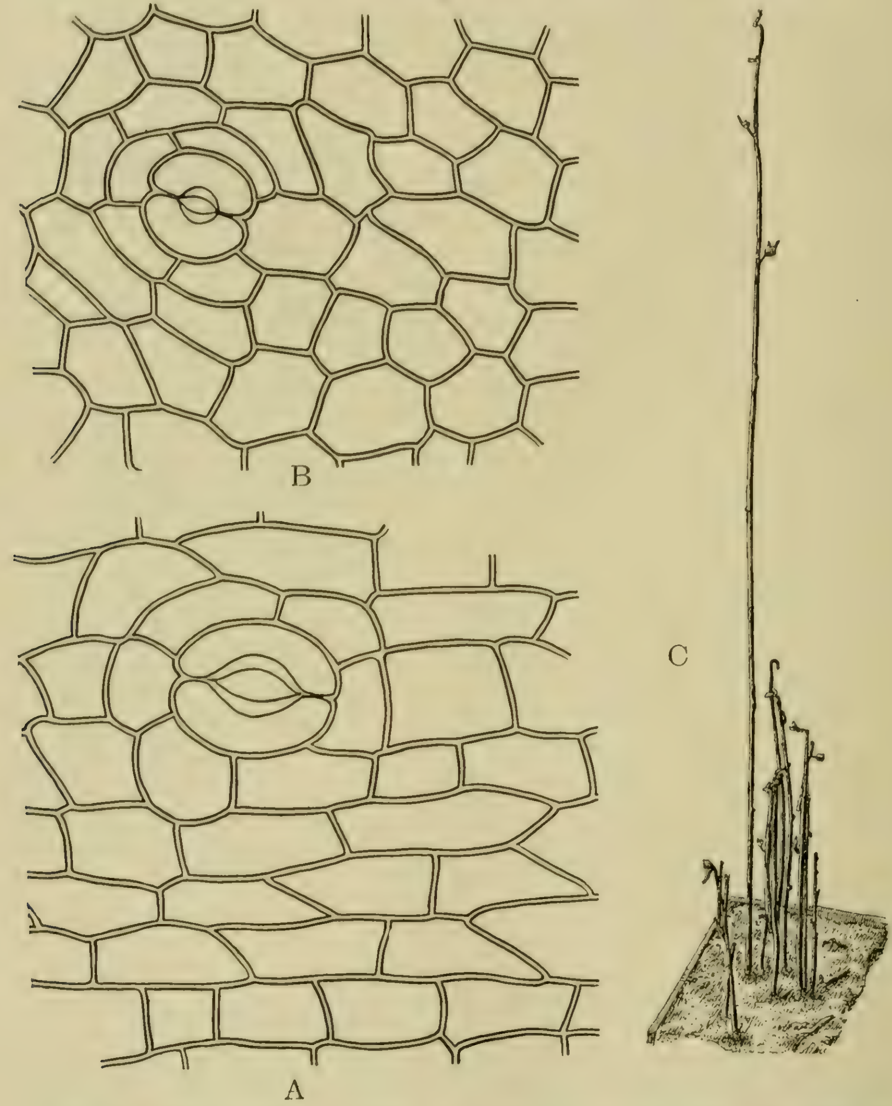

Fig. 82. *Menispermum Canadense.* *A*, epidermis of normal stem; *B*, epidermis of etiolated stem. Etiolated culture.

that the ordinary aërial stems usually form but few leaves before reaching a length of a meter or two, hence this is a vine which does not show excessive elongation, or suppression of organs to any marked extent, in etiolation of awakening shoots. The epidermal cells were smaller in all dimensions than the normal, and the stomata which seemed to be present in normal numbers were functional. The hairs were hardly so numerous as in the normal. A normal collenchymatous subepidermal layer was lacking in the etiolated stems, and the cortex showed an increase both in number and size of the elements, and contained no intercellular spaces in either instance. The etiolated cortex showed five to eight layers of cells and the normal but three or four.

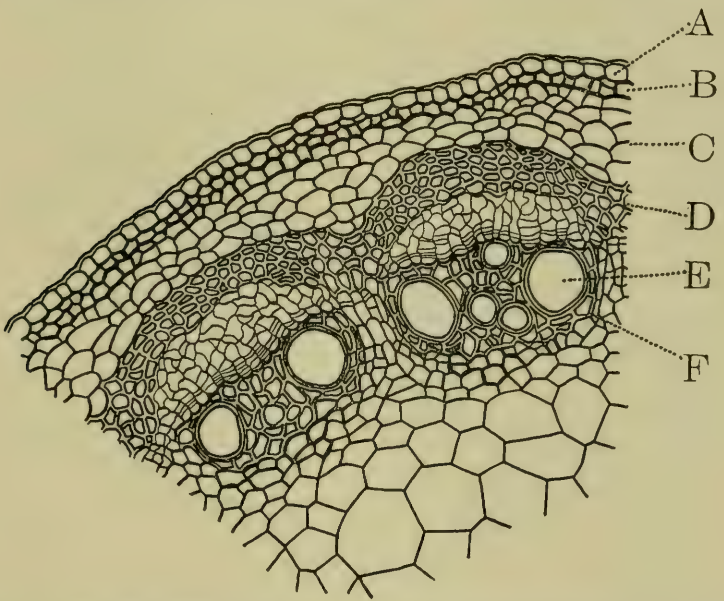

FIG. 83. *Menispermum Canadense.* Partial transverse section of normal stem. *A*, epidermis; *B*, subepidermal layer; *C*, cortex; *D*, bast fibers; *E*, xylem; *F*, xylem parenchyma. Cambium and sieve tissue are to be seen between *D* and *E*.

The bast fibers formed a complete cylinder in the normal, while in the etiolated stem they are represented by elongated elements with walls but little thicker than the cortical cells, and the groups external to the separate bundles did not fuse or extend into each other. The sieve cells seemed to be quite as well differentiated in the etiolated specimen as in the normal, although not so numerous, and the lumina were not so great, as if these elements had taken on mechanical as well as conductive functions. The xylem offered as many vessels as in the normal, but these did not reach the size of the normal, and a noticeable lack of development of the intravascular parenchyma was to be seen. Extremely large intercellular spaces were to be seen in the pith of the etiolated stems. The cambium cylinder, composed of two or three layers in both normal and etiolated stems, appeared to form a continuous cylinder in the etiolated stem, but was interrupted by the heavy rays in the normal.

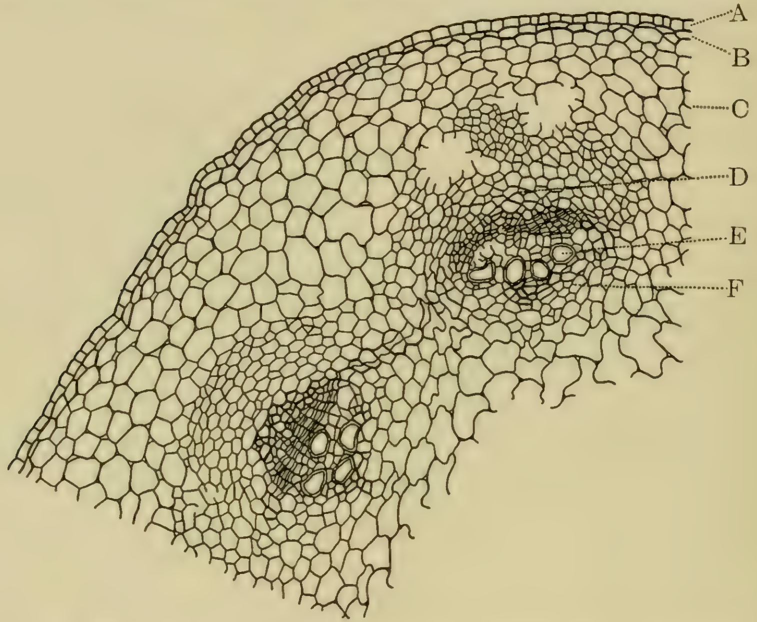

FIG. 84. *Menispermum Canadense.* Partial transverse section of etiolated stem. Description as in Fig. 83.

This vine behaves in accordance with Sachs' conclusions that vines are etiolated stems, but the lack of development is probably due to lack of nutrition. Twining was not observed in any of the stems of the numerous cultures. Many of the rhizomes were alive after the first growth in darkness, but cultural conditions did not permit a second growth.

Narcissus Tazetta L.

A large number of etiolations were made of *Narcissus* from bulbs obtained from dealers during the period 1896–1902. Bulbs of *N.*

nana, *N. poeticus* and *N. tazetta* were cultivated in the dark chambers and the results obtained from the three species were so nearly uniform that no separate discussion is needed for each.

The leaves attained a length more or less in excess of the normal in all instances, and showed a somewhat attenuated epidermis with functional stomata. The air spaces were not so large as in the normal, and the sheathing scales at the base were longer. The leaves normally assume a position nearly erect, but in the etiolated plants these organs soon become decumbent and prostrate. Their width is fully equal to that of the normal.

The inflorescence axis normally exceeds the leaves in length, or attains a length about equal to them. The stalks show a large lysigenetic central cavity which was not so large in the etiolated stalks. The etiolated inflorescence axes did not reach a length of more than half of the normal, and the flowers scarcely advanced beyond the stage in which they are to be found in the normal buds just emerged from the bulbs. The inflorescence was enclosed in a complete sheathing scale which did not open. In no instance did the flowers emerge or assume a normal aspect.

Onoclea sensibilis L.

Rhizomes of *Onoclea* taken from the soil in March, soon developed long stipes with the laminar portion rolled up. The stipe reached a length of 70 to 80 cm., while in the normal it did not measure more than half this length. The increase in length was accompanied by an excessive increase in thickness due to the exaggeration of the fundamental tissue. The gamosteles were

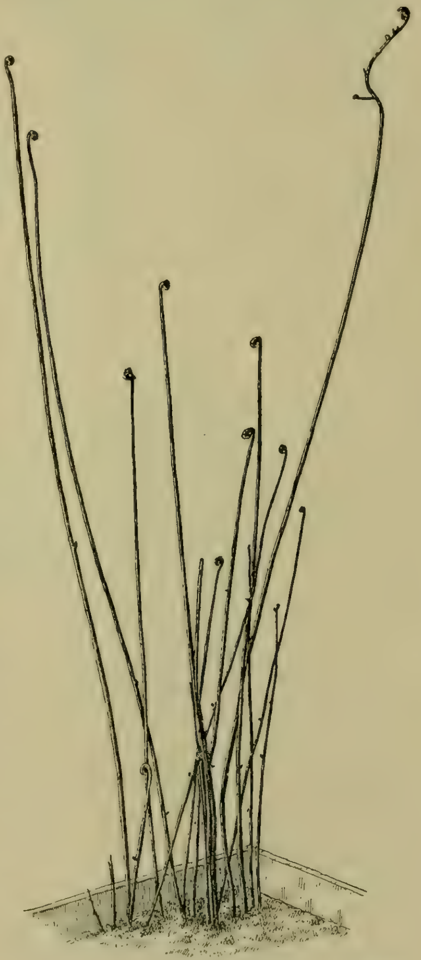

FIG. 85. Etiolated culture of *Onoclea sensibilis*.

fairly normal but did not fuse until a greater distance from the base than usual had been reached. The sclerenchymatous external layers, including the epidermis, showed less thickening, to which was due the greater pliability of the etiolated stems. A few of the stalks of the lower pinnae were elongated, but in every instance the foliar or laminar tissues remained in a clump or bunch.

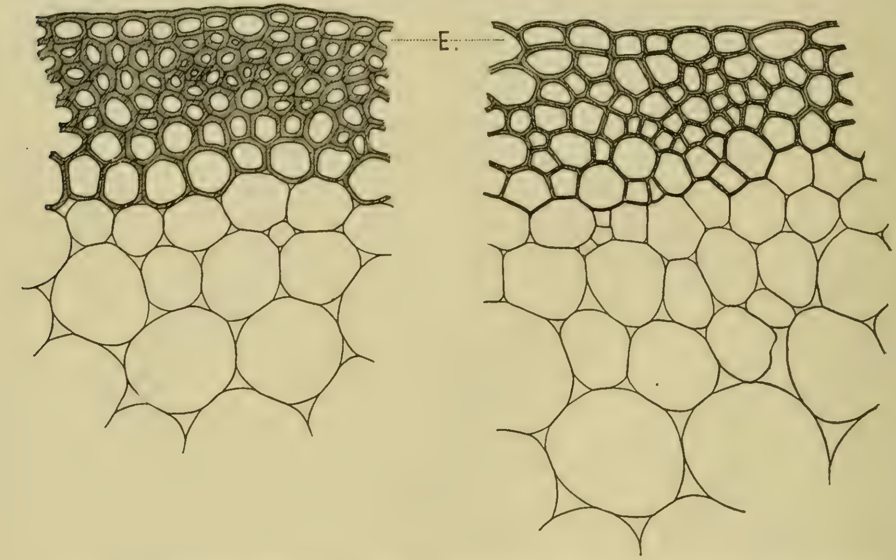

FIG. 85. *Onoclea sensibilis.* Partial transverse section of normal and etiolated stipe. *E.* epidermis.

Etiolation is thus seen to result in an excessive elongation of the stipe in the basal portion. The rhizomes were not exhausted by the growth of etiolated fronds, and appeared capable of making a second effort to reach light.

Ornithogallum umbellatum L.

Bulbs of *Ornithogallum* placed in the dark chamber in January, 1901, developed leaves with a length of 22 cm. within a month. The leaves were crescentic in cross section, many of them twisted and about 6 mm. in breadth when flattened. The flower bud remained dormant during the entire confinement to darkness, and when the preparations were brought into light after two months, the leaves showed some decay at the tips, but made an increased growth, while the flower bud remained inactive.

The bulbs were not exhausted by this treatment, and seemed capable of making a second growth in darkness.

Opuntia Opuntia (L.) Coult.

A number of fronds of *Opuntia Opuntia* were laid flat on moist soil in the dark room, in November, 1901, and had developed cylindrical or compressed stems, which were slightly longer than the normal by January 6, 1902. The leaves, which are subulate and fall off early in the normal, were of an attenuated ovoid form, being drawn down to a very small diameter both at the base and apex. These leaves persisted until the etiolated stems began to show signs of deterioration, when they were easily detachable.

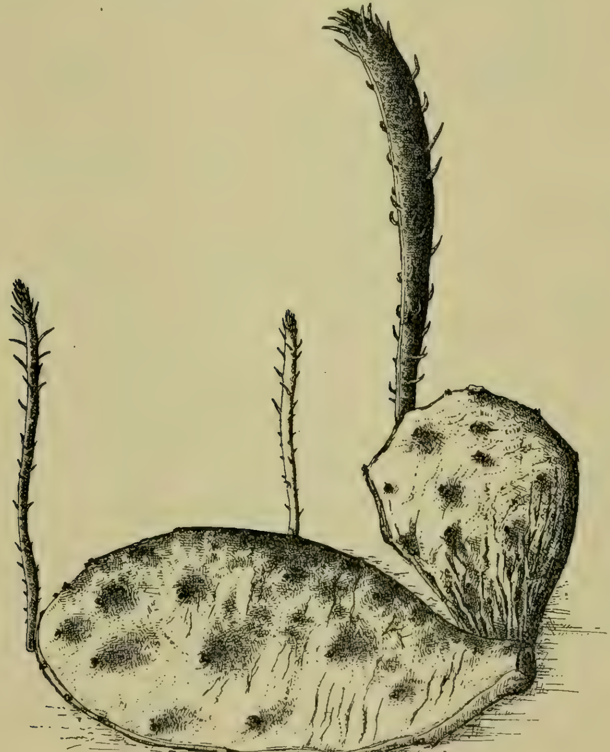

FIG. 87. *Opuntia.* Prostrate normal frond, from which arise etiolated stems.

Marked deviations from the normal were to be seen in the structure of the leaves. Numerous multicellular hairs were found around the leaves, but very few bristles were to be seen. The epidermal cells including the stomata were reduced in size in etiolated plants, and the arrangement of outer layers rich in chlorophyl with their long axes at right angles to the surface was noticeably lacking in etiolated stems, in which no differentiation was to be seen except in the development of one or two layers of smaller cells beneath the epidermis. These cells contain a large number of globular clusters of crystals in the normal, which are not nearly so numerous in the etiolated fronds. The outer walls of the epidermis were less thickened in the etiolated.

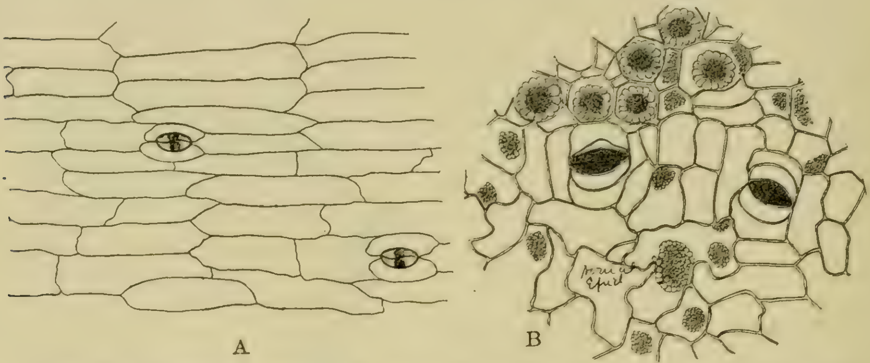

FIG. 88. *Opuntia Opuntia*. *A*, etiolated epidermis, surface view; *B*, normal epidermis, surface view.

Osmunda cinnamomea L.

Clumps of *Osmunda* brought into the dark room in April, 1900, soon developed long straggling fronds thickly clothed with pale hairs, with pinnae extended but not attaining a length in excess of 1.5 cm. The entire frond showed a distinct greenish tinge due to the presence of a marked amount of chlorophyl. The outer tissues including the epidermis were much less thickened than the normal, the epidermal cells being notably elongated and containing chloroplasts. Functional stomata were present and contained many chloroplasts.

The parenchymatous tissues as in the normal showed some intercellular spaces, but the walls were more or less wavy. The endodermis (phloeoterma) was made up of smaller elements with less thickened walls than in the normal. The pericyclic cells were not to be distinguished from the sieve cells or the adjoining parenchyma. The mass of tissue between the endodermis and metaxylem, usually consisting of the pericycle, the parenchyma separating it from the sieve tissue, and the parenchyma between the sieve tissue and the metaxylem, was much thinner than in the normal, and it was not possible to determine which of these tissues was lacking. The metaxylem was but little different from the normal. The walls of the protoxylem (consisting of groups of small cells immediately inside of the xylem) were not so much thickened as in the normal. The in-

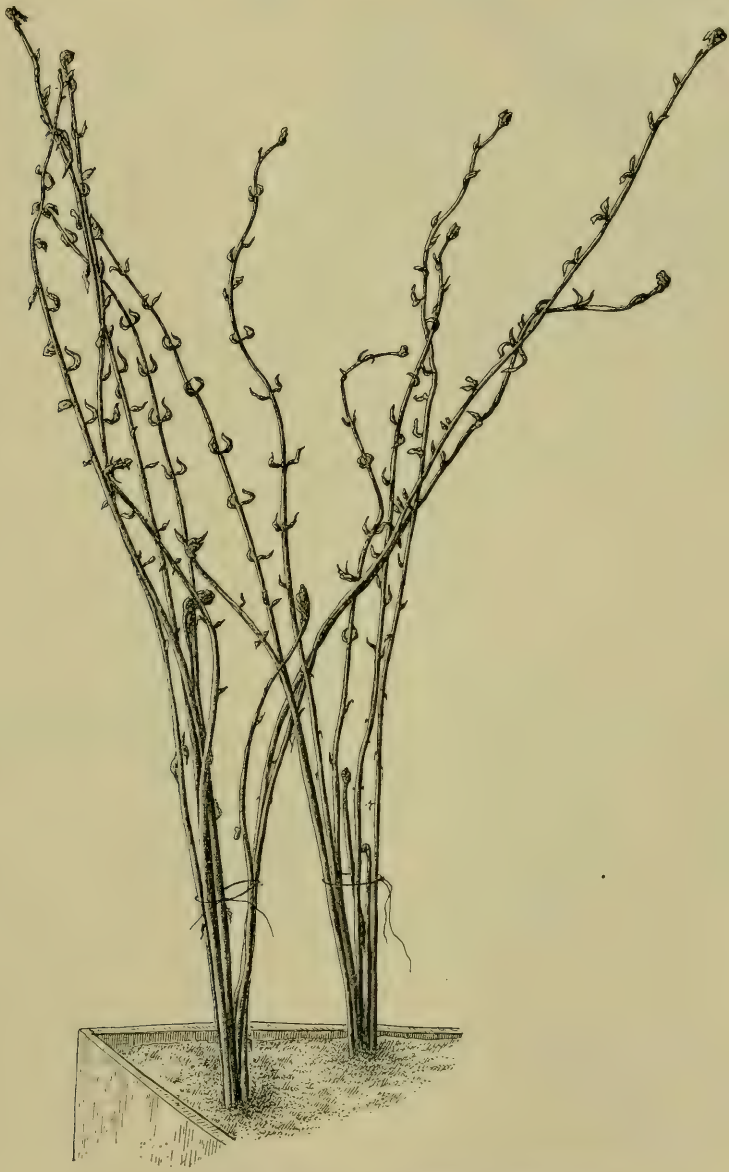

FIG. 89. Etiolated culture of *Osmunda cinnamomea*.

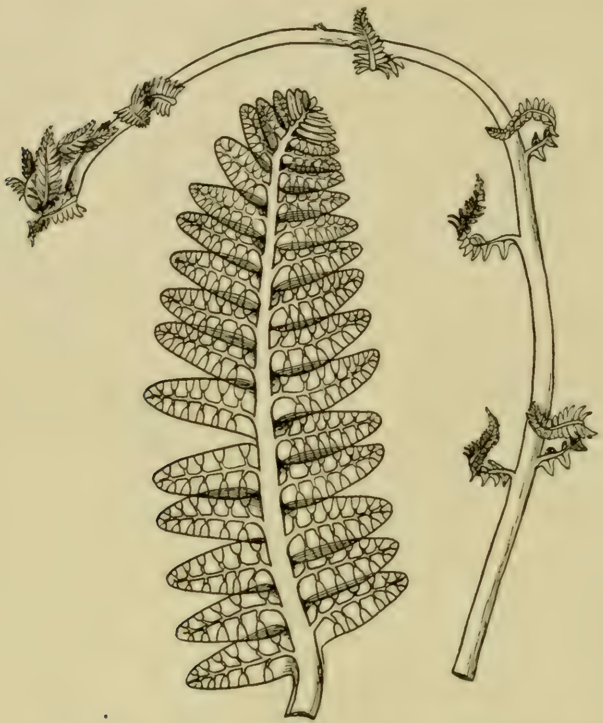

FIG. 90. *O. cinnamomea.* Terminal portion of etiolated frond, and single pinna.

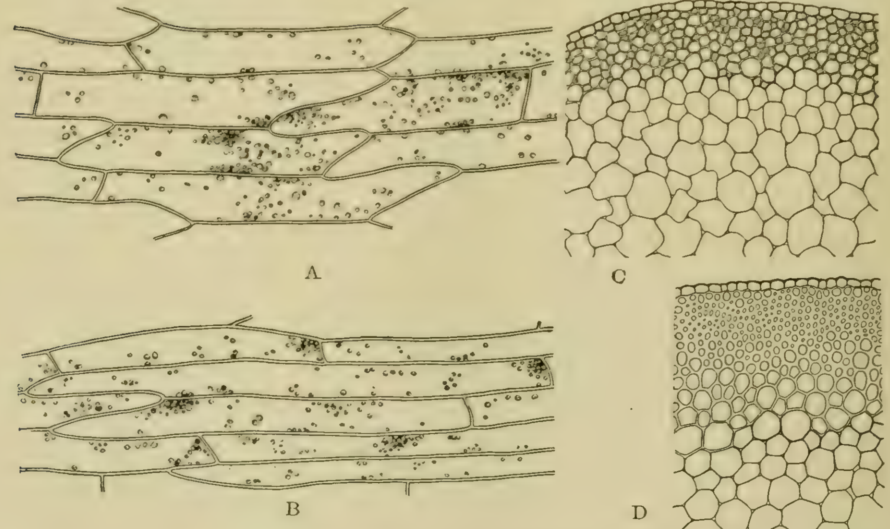

FIG. 91. *Osmunda cinnamomea.* *A*, normal epidermis, surface view; *B*, etiolated epidermis, surface view; *C*, partial transverse section of etiolated stipe; *D*, partial transverse section of normal stipe.

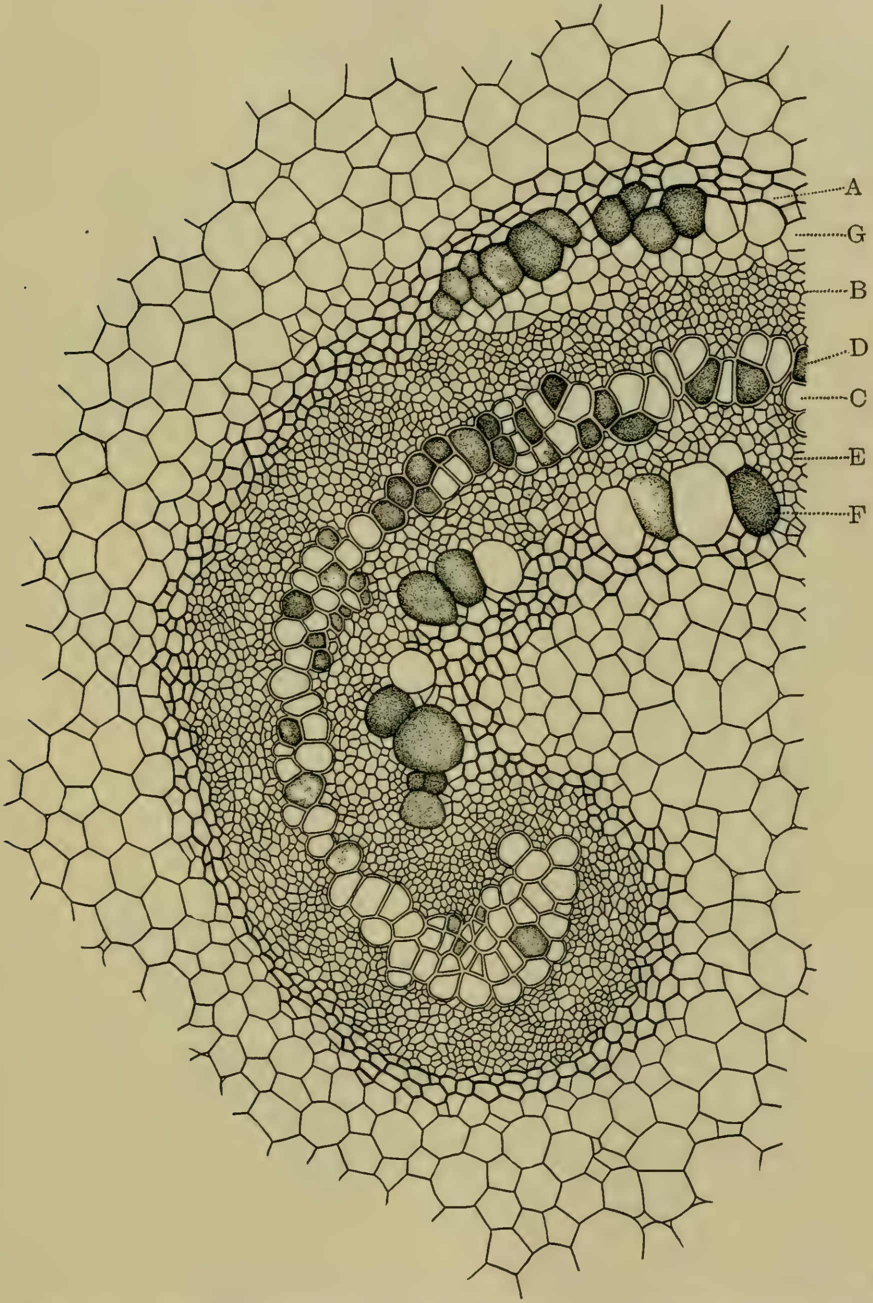

FIG. 92. *Osmunda cinnamomea.* Transverse section of portion of normal stelar region. *A*, endodermis (phloeoterma); *G*, specialized group of pericyclic cells containing tannin; *B*, *E*, sieve tubes; *C*, *D*, metaxylem; *F*, pericycle and tannin cells in this tissue.

ternal sieve tubes were larger than in the normal and with lighter or thinner walls. The endodermis internal to the sieve cells just mentioned was less heavily thickened than in the normal, and was not to be separated from the pericycle bounded by it.

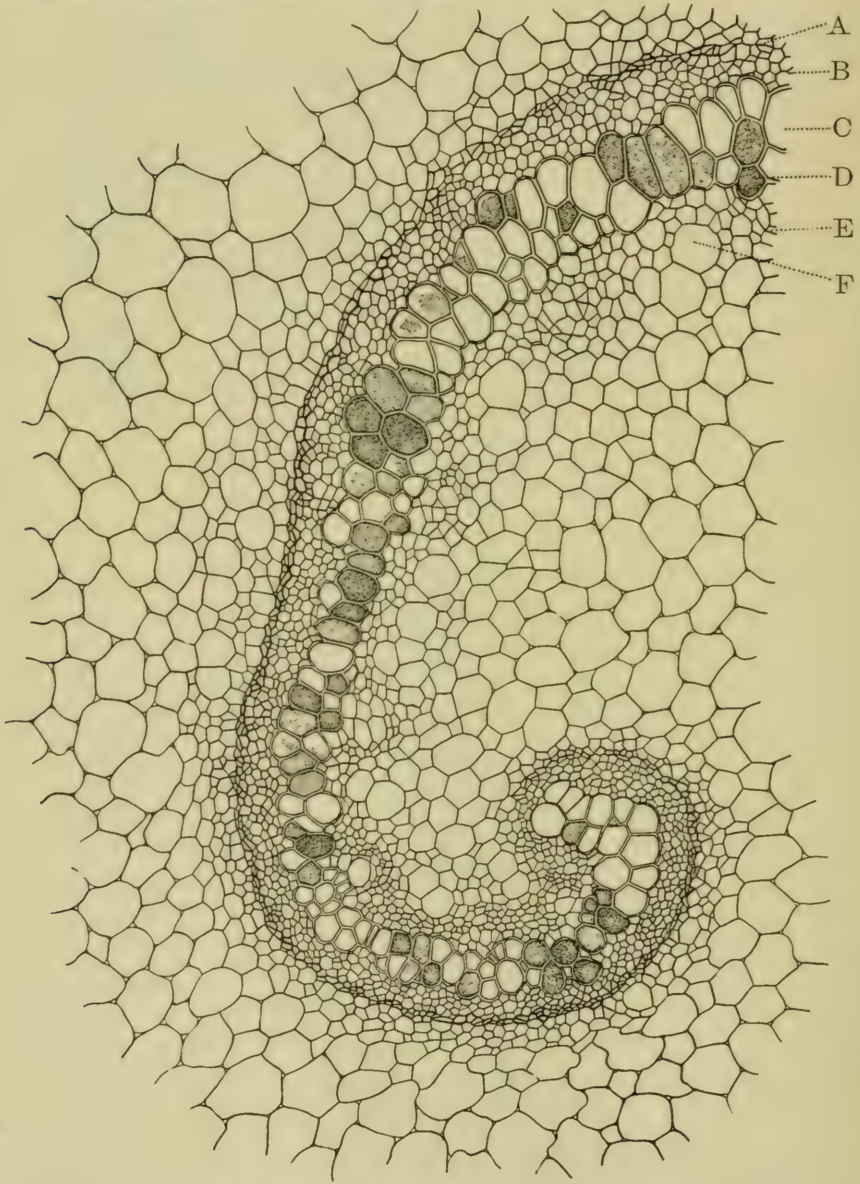

FIG. 93. *Osmunda cinnamomea.* Transverse section of portion of etiolated stelar region correspondent to that shown in Fig. 92. Description as in Fig. 92.

Oxalis lasiandra Zucc.

Bulbs of *Oxalis lasiandra* placed in the dark chamber at various times were compared with cultures in very diffuse light, and in daylight. The first activity was shown in the development of leaves with elongated petioles and some offsets. The roots did not break out until later. The length of the petioles was as much as 11 or 12 times that of the normal in some examples, while in others it might not reach more than double the length of the normal. In one series of tests the average length of normal petioles was 20.87 cm., in diffuse light 36.9 cm., and in darkness 47.1. The thickness in normal and

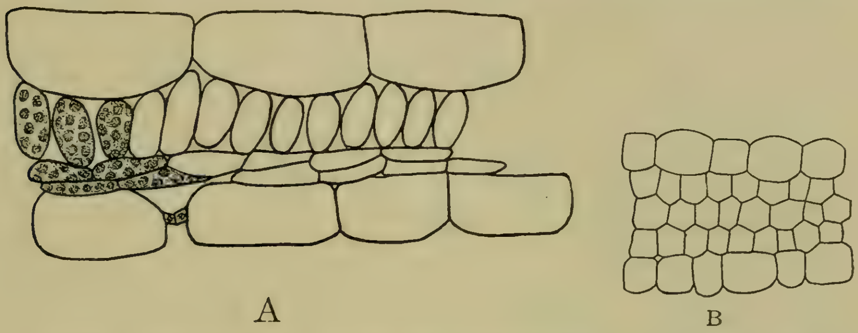

FIG. 94. *Oxalis lasiandra*. Transverse sections of leaf. *A*, normal; *B*, etiolated.

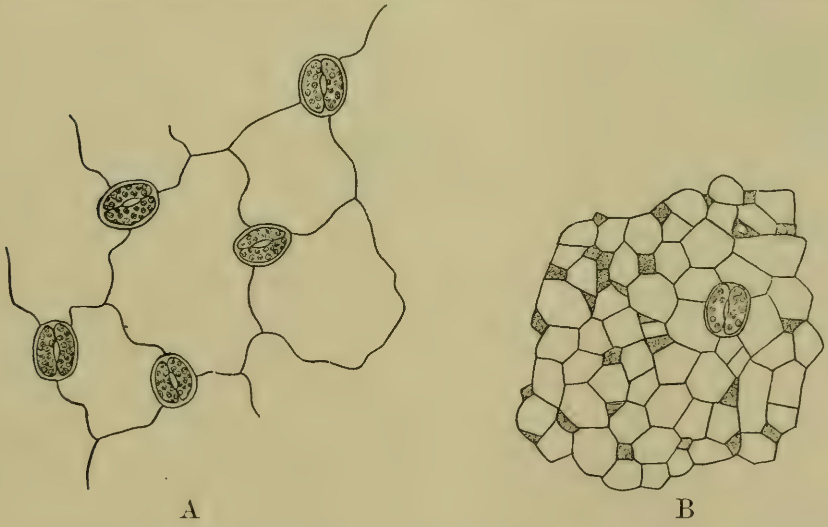

FIG. 95. *Oxalis lasiandra*. Surface view of epidermis of leaf. *A*, normal; *B*, etiolated.

etiolated specimens was about the same, but those in diffuse light were much heavier, probably in response to the mechanical stimulus of the weight of the leaflets. The laminae remained in the folded condition in which they emerged from the bud, in the etiolated examples, and attained only about one fifth of the volume of normal examples.

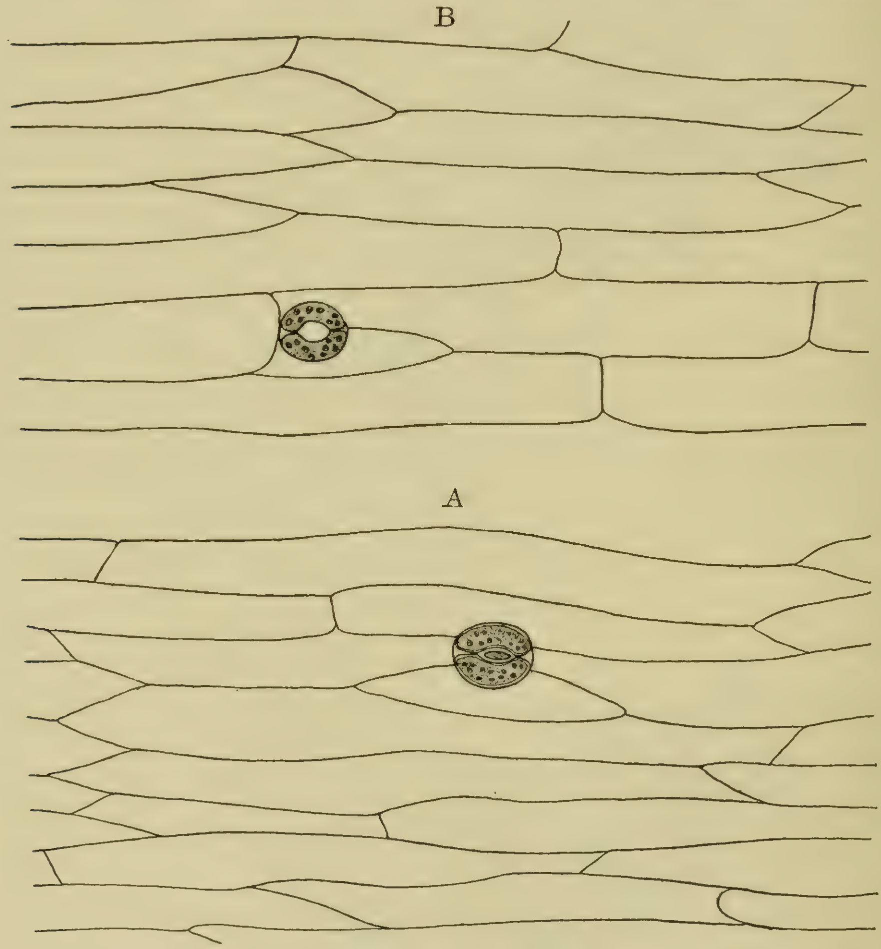

FIG. 96. *Oxalis lasiandra*. Surface view of epidermis of petiole, *A*, etiolated; *B*, normal.

The epidermal cells of the etiolated petioles had an average measurement of 127.4 as compared with the normal of 129.1, and a width of 4.91 as compared with the normal at 6.14. The number of stomata included in a microscopic field from the etiolated specimen at one time was on an average 1.4 and in the normal specimen 2.2, the etiolated measuring 6.82 by 9.56, while the normal measured 9.6 by 7.12, showing that while the size of the etiolated epidermal elements was smaller than in the normal, the number of epidermal cells had increased to meet the excessive elongation of the petiole, but this multiplication has not been followed entirely by the stomata, although some increase has been made.

The cortical cells of the petioles gave measurements comparable to those of the epidermis, being 163.45 by 29.5, while the normal were 168.75 by 43.75, showing here also a multiplication of elements. The bast cells in the etiolated were 10.9 by 9.35, while the normal were 11.05 by 9.19, showing a diminution in length, but a slight increase in thickness. The walls are all thinner and only traces of lignification were found in the xylem.

The stomata on the leaflets measure 5 by 5.13 in the etiolated and 6.88 by 9.1 in the normal, showing an average of 6 in the field in the etiolated, and 8.6 in the normal. A number of pre-stomatal elements were to be seen in the etiolated laminae, which never underwent the final stages of development in darkness.

The hairs on the etiolated leaves measure 281.25 by 5.05 in the etiolated and 128.125 by 4.95 in the normal, thus exhibiting excessive elongation, and but little increase in diameter. The marginal epidermal cells of the leaf measured 6.64 by 5.92 in the etiolated specimen and 25.3 by 8.35 in the normal. The epidermis of the upper surface measured 5.51 by 4.13 by 4.26 in the etiolated leaflet and 30.96 by 20.8 by 15.95 in the normal. Epidermal cells from the lower surfaces measured 5 by 3.97 by 4.95 in the etiolated and 29.28 by 20.4 by 9.2 in the normal, from which it is to be seen that an increase in the actual number of cells follows etiolation in the leaflets, as well as in the petioles. Differentiation into palisade and spongy parenchyma did not ensue in the etiolated leaflet.

The following determinations of ash, dry matter and water in *Oxalis lasiandra* were made:

I. NORMAL LEAVES INCLUDING PETIOLE.

Weight of fresh material	3.13	grams.
" dry "	.219	"
" ash "	.021	"
Percentage of water	93.	
" dried matter	7.00	

Percentage of ash in fresh material	.67	
" " dried "	9·59	

II. ETIOLATED LEAVES INCLUDING PETIOLE.

Weight of fresh material	·434	gram.
" dried "	.019	"
" ash "	.003	"
Percentage of water	95·62	
" dried matter	4·38	
" ash in fresh material	.69	
" " dried "	15·78	

V. LEAVES GROWN IN DIFFUSE LIGHT.

Weight of fresh material	1·358	grams.
" dried "	.058	"
" ash "	.003	"
Percentage of water in fresh material	95·73	
" dried matter	4·27	
" ash in fresh material	.221	
" " dried "	5·17	

VI. NORMAL BULBS.

Weight of bulbs bearing leaves, fresh	·599	gram.
" dried material	.127	"
" ash	.006	"
Percentage of water	79·65	
" dried matter	20.35	
" ash in fresh material	1.001	
" " dried "	4·724	
Weight of resting bulbs	2.685	grams.
" dried matter	1.252	"
" ash	.020	"
Percentage of water	53·37	
" dried matter	46.63	
" ash in fresh material	·745	
" " dried "	1·597	

VII. ETIOLATED BULBS.

Weight of bulbs bearing etiolated leaves	1·394	grams.
" dried matter	·591	"
" ash	.006	"
Percentage of water	56.13	
" dried matter	43·87	

Percentage of ash in fresh material	.446	
“ “ dried material	1.02	

VIII. Bulbs in Diffuse Light.

Weight of bulbs bearing leaves, grown in diffuse light	1.88	grams.
Weight of dried material	.666	“
“ ash	.014	“
Percentage of water	64.58	
“ dried matter	35.42	
“ ash in fresh material	.744	
“ “ dried “	2.102	

III. Etiolated Leaves and Bulbs.

Weight of etiolated leaves	2.571	grams.
“ “	.100	“
“ “	.005	“
Percentage of water	96.08	
“ dried matter	3.92	
“ ash in fresh material	.194	
“ “ dried “	5.	
“ water in bulbs bearing etiolated leaves	64.94	
Percentage of dried matter	35.06	
“ ash in fresh material	.634	
“ “ dried “	1.77	

IV. Etiolated Leaves.

Weight of leaves, etiolated	1.904	grams.
“ dried material	.079	“
“ ash	.005	“
Percentage of water	95.85	
“ dried matter	4.15	
“ ash in fresh material	.262	
“ “ dried material	6.33	

Oxalis violacea L.

Etiolated leaves of *Oxalis violacea* developed petioles 6 to 20 cm. in length which were about .75 mm. in diameter at base and 1 to 1.25 mm. in diameter at upper end. The relations between the dimensions of epidermal cells of normal and etiolated petioles were the same as in *O. lasiandra*. Stomata were present, some of them functional, in the etiolated examples, and the guard cells were always filled with starch. The epidermal and hypodermal layers as well as the cortex did not differ greatly from the normal except that the elements of the cortex had a greater radial measurement than in the normal. The three bundles in the petiole were separated by two or three layers of parenchyma in the etiolated, and by but one in the normal. On the other hand the larger vessels were separated from each other by one or more layers of parenchyma in the etiolated while they appeared in contact in the normal. The sieve tissue seemed more irregularly developed in the etiolated. The laminae

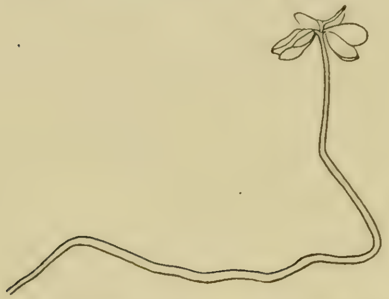

FIG. 97. *Oxalis violacea*. Etiolated leaf after a few days' illumination.

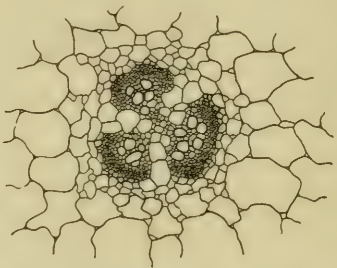

FIG. 98. *Oxalis violacea*. Transverse section of stelar region of normal petiole.

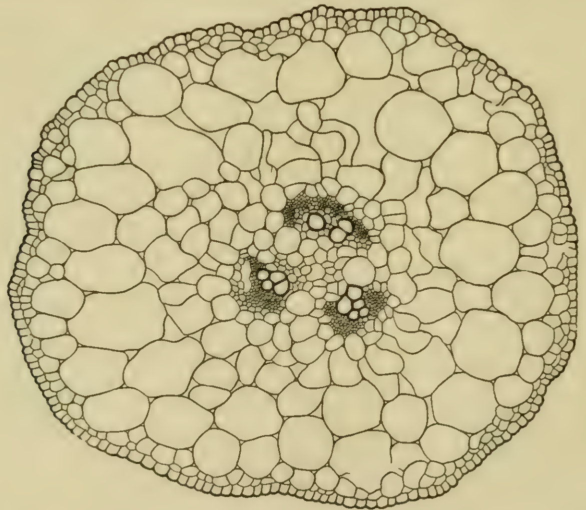

FIG. 99. *Oxalis violacea*. Transverse section of etiolated petiole.

of the leaflets remained folded together, and were thickly furnished with hairs. A large quantity of a reddish coloring matter was noted. The bulbs were healthy and small; new ones were formed in both species of *Oxalis* examined. After the production of the first lot of etiolated leaves, growth was confined to the development of runners or offsets.

Pastinaca sativa L.

Parsnips were placed in the dark chamber in January, 1901, and sent up leaves which had reached full size on April 11, 1901. The petiole and its main branches in the leaf showed excessive elongation. The petiole measured 25 cm. from the stem to the first pair of branches, 6 cm. between the first and second pair of branches of the petiole, and 3 cm. between the second and third pairs. The distance between the third and fourth pairs amounted to about a centimeter, and the terminal branches were irregularly arranged. The laminae were extremely small and were of a deeper yellow than most etiolated organs.

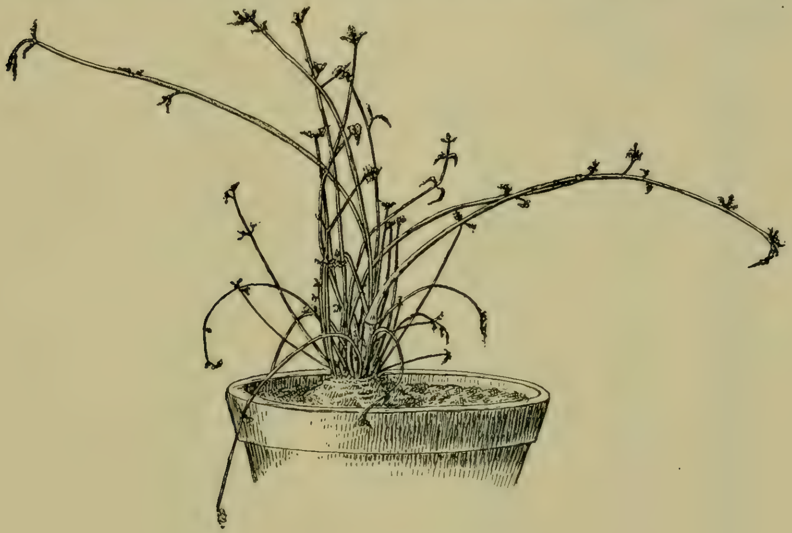

FIG. 100. Etiolated culture of *Pastinaca sativa.*

It was found that the size of a leaflet, or the length of the petioles might be increased beyond the average of etiolated organs, by cutting away concurrent organs which would compete for the food supply. The laminae were furnished with many perfect stomata, but no starch was seen here, or in any other part of the leaf. The leaves began to perish within a fortnight after maturity, and the rootstock died also.

Peltandra Virginica (L.) Kunth.

Corms which showed signs of activity in April were brought into the dark chamber. A month later the petioles had reached a height of 25 to 30 cm. and the lamina were unrolled but variously inclined to the vertical. The laminae reached a length of 14 to 16 cm. and a width of 4 to 6 cm. or about half the maximum dimensions.

The petioles were more slender than the normal. The lower surfaces of the leaves showed a large number of open stomata which remained open when examined in water, the guard cells being filled with starch. This substance was also abundant in the region contiguous to the nerves. The structure of the leaves was fairly approximate to that of the normal. The upper surfaces presented a number of stomata, but like the normal were not so numerous as on the lower. But little difference between the structure of the etiolated and normal petioles could be found, except perhaps in the size of the parenchymatous cells, which were smaller. Similar re-

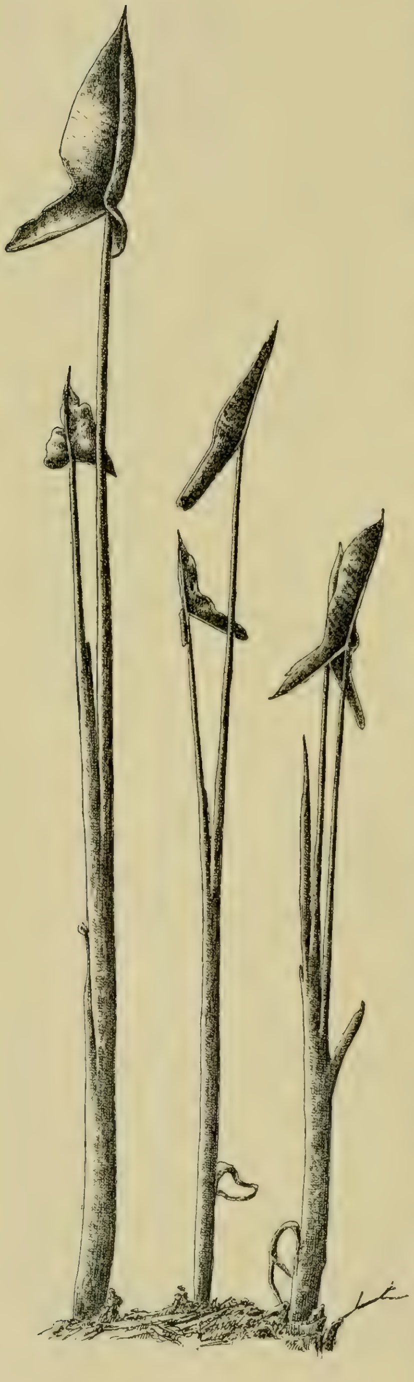

FIG. 101. *Peltandra Virginica.* Etiolated culture.

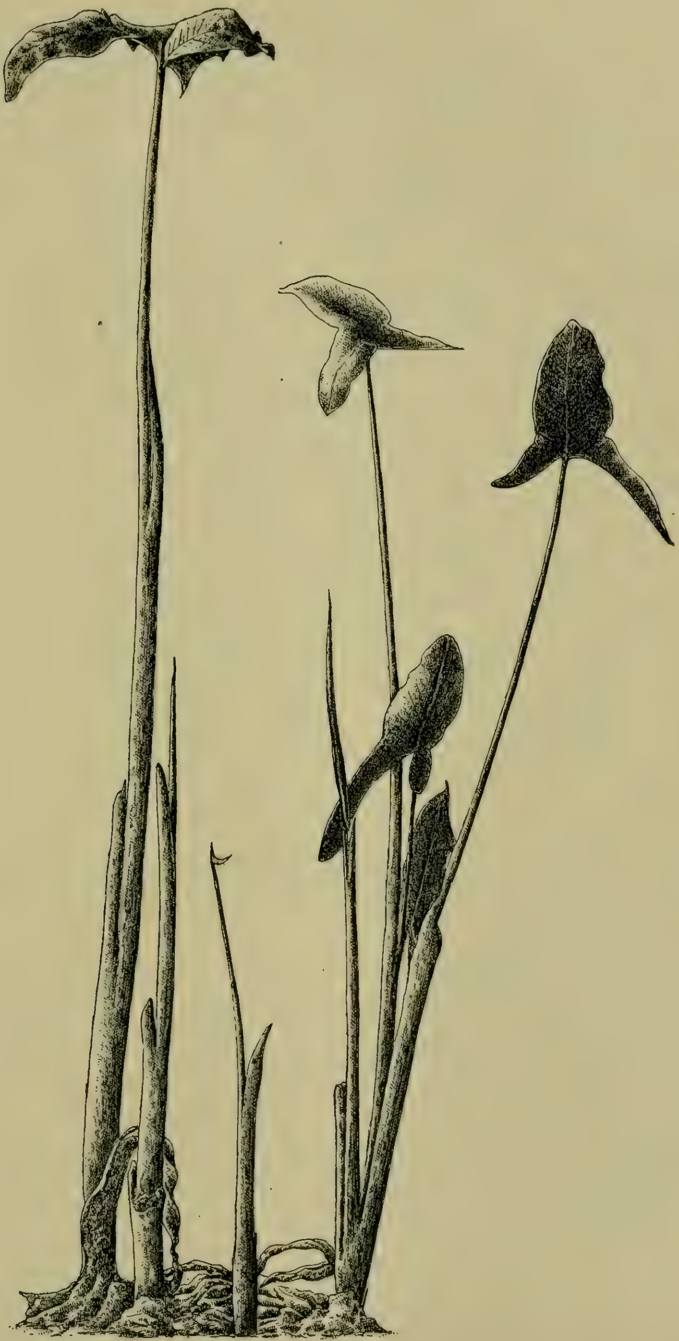

FIG. 102. *Peltandra Virginica.* Etiolated culture shown in Fig. 101, after ten days' exposure to illumination.

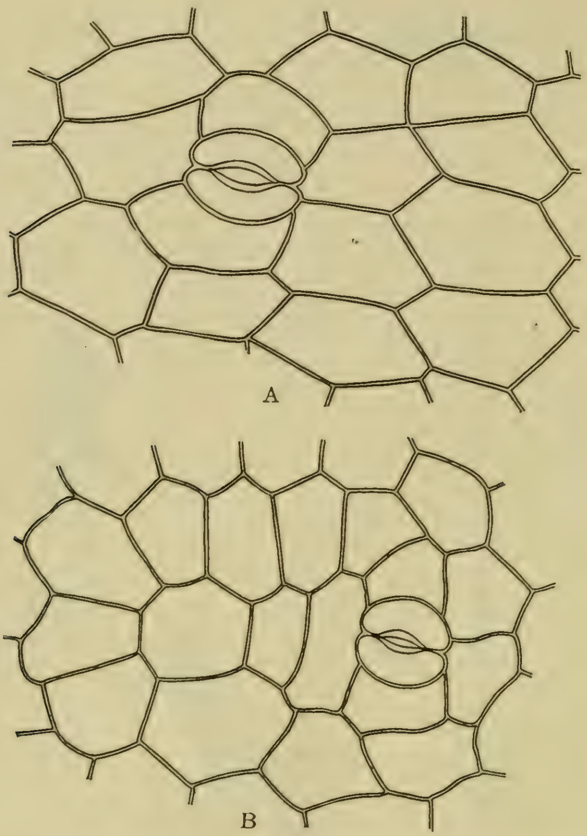

FIG. 103. *Peltandra Virginica.* *A*, epidermis from ventral surface of normal leaf. *B*, epidermis from ventral (inner) surface of etiolated leaf. × 250.

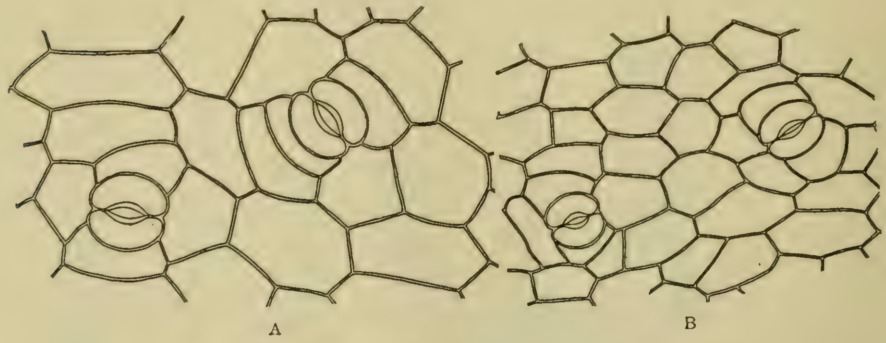

FIG. 104. *Peltandra Virginica.* *A*, epidermis from dorsal surface of lamina, normal. *B*, epidermis from dorsal (outer) surface of etiolated lamina. × 300.

sults were obtained from the study of a number of plants at different times.

A fully etiolated specimen of *Peltandra* which was brought into diffuse daylight, showed some marked changes as the result of illumination, among which were to be noted the assumption of the horizontal position of the laminae, and the unequal development of the basal lobes which ensued under such conditions.

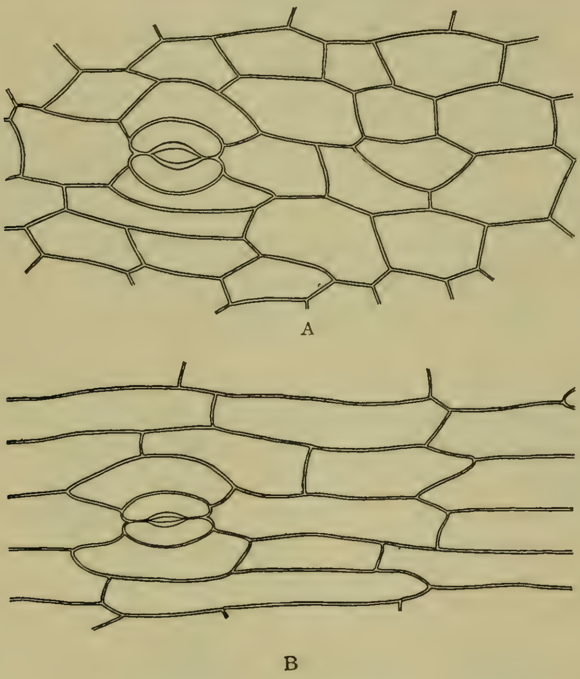

FIG. 105. *Peltandra Virginica*. *A*, epidermis from normal petiole. *B*, epidermis from etiolated petiole.

Peltandra is a bog plant, or rooting aquatic, according to circumstances.

Phaseolus sp. (cultivated).

Numbers of seedlings of *Phaseolus* were etiolated with the invariable result that the first internode attained a length about three times the normal, when proper cultural conditions were furnished. The first pair of leaves developed petioles over a centimeter in length, and laminae of equal length. The entire shoot of the seedlings attained an extreme length of 30 cm., the terminal portion above the single pair of leaves being about 6 cm. long, with recurved apex. The stalks were generally more or less compressed and flattened.

In other tests the terminal portions of large plants were conducted into small dark chambers to secure "partial" etiolations. Branches treated in this manner developed flowers which were fairly normal, except that they were blanched. The essential organs were perfect, and fertilization ensued, pods and seeds being formed. The latter were apparently perfect, but no germination tests were successful. The leaves were entirely devoid of chlorophyl, but the leaflets were held in various positions with the upper surfaces concave, and did not exhibit the nyctitropic movements, so far as my observations went, although particular attention was not paid to this point.

It is to be seen that the effects of "partial etiolation" differ most widely from those in which the entire plant is deprived of light. In partial etiolations

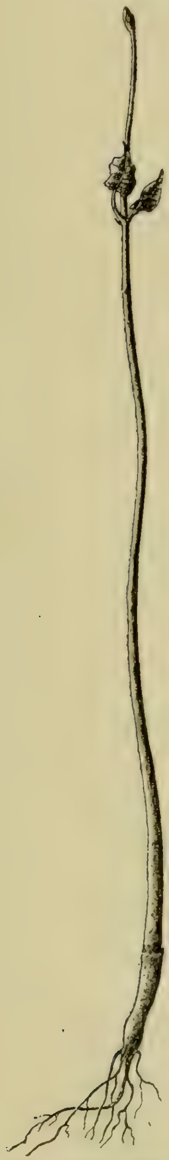

FIG. 106. Etiolated seedling of *Phaseolus*.

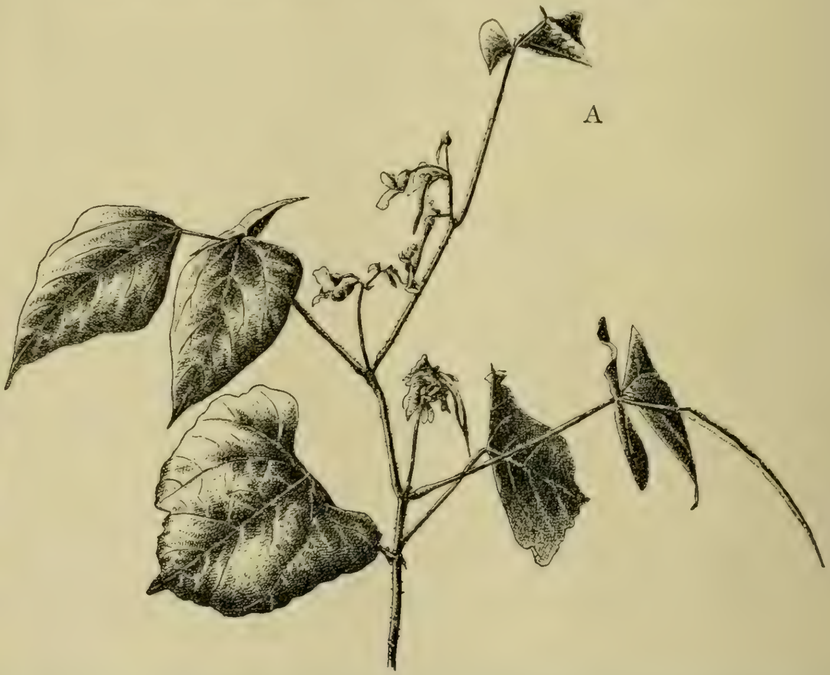

FIG. 107. Terminal portion of shoot. The branch *A*, has been enclosed in a small dark chamber and bears leaves, flowers and young pods formed under these conditions.

it is difficult to furnish absolute security against admission of light, and the darkened portion is probably influenced by the illuminated regions near it.

Phytolacca decandra L.

A number of strong roots of pokeweed were taken from the soil in a resting condition in November and placed in pots in the control house, and dark room immediately. Growth began about a month later. The shoots produced in the dark chamber elongated much more rapidly than those under normal illumination and had attained a length of 22 cm. on January 22, 1902. Shortly afterward these shoots perished and others sprang up from the crown, which likewise made only a limited growth. This process was repeated, and on April 27 four etiolated shoots were to be seen with others beginning to develop. On July 6th the stems had reached a length of 42 cm., with leaves 45 cm. long. The tuberous underground storage organ remained intact and seemed sound and healthy.

The diameter of etiolated stems did not exceed 11 mm., which is much less than the normal. The cross section was ovoid in outline although lacking the small irregularities of that of the normal stem. The etiolated leaves consisted of a small slightly elongated petiole curved upward from a horizontal position with a much reduced lamina. The entire leaf was a rich yellow color.

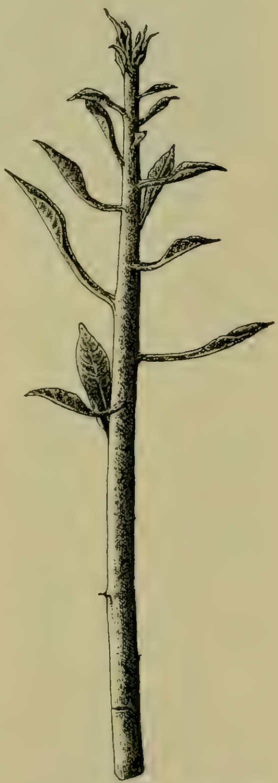

FIG. 108. Etiolated stem of *Phytolacca decandra*.

The pith showed the transverse splittings of the normal stem in the basal portion, but in the terminal portion a long continuous cavity occupied the center of the stem. The epidermis was not excessively elongated and had comparatively thin walls. The prestomatal cells were to be seen richly loaded with granular matter and plastids and in some instances the first division had taken place. The collenchyma was fairly well developed in the angular portions of the stem occupying about six or seven layers, in some instances and but two or three in other places. The cortex was composed of extremely thin walled elements with some intercellular spaces.

The protoxylem was fairly normal but the woody tissue was very imperfectly developed, while the formation of the secondary wood ring and xylem had only progressed so far as to show groups of elements with denser contents in the positions of the vessels, and the presence of a layer of cambiform calls external to them. Numbers of elongated lenticellular ridges appeared on the basal portion of the stem in the region from which the leaves had fallen.

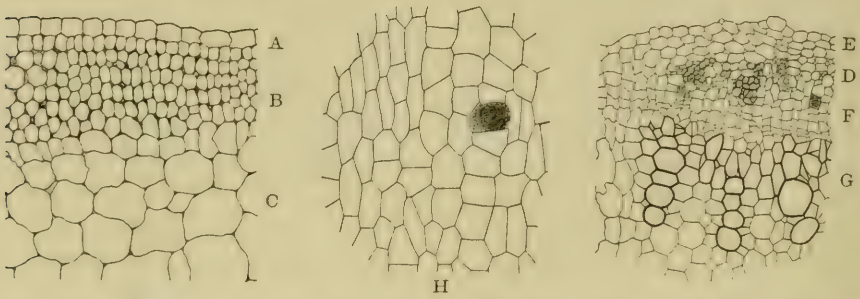

FIG. 109. *Phytolacca decandra.* Structure of etiolated stem. *A*, epidermis; *B*, collenchyma; *C*, cortex; *D*, bast fibers; *E*, location of secondary cambium; *F*, cambium; *G*, xylem; *H*, surface view of epidermis, showing one prestomatal cell.

The comparatively brief duration of the shoot was coupled with the non-formation of stomata on the stem.

Podophyllum peltatum L.

Rootstocks of *Podophyllum* were brought into the dark room at various times and the leaves and flowers allowed to develop.

Petioles showed an elongation about 80 per cent. in excess of the normal and the epidermal elements were correspondently elongated. The lobes of the centrally peltate leaves were about one third the length of the normal, and were folded with the under surfaces together, the whole etiolated laminae having the form of a partially opened umbrella. Stems bearing both leaves and flowers reached a length about double the normal in darkness, and the flowers were fairly normal in structure opening partially. The lack of functional maturity of the stomata was accompanied by a brief duration of the leaves and stalks, and the etiolated organs soon perished, resting buds being formed on the rootstocks which could not be awakened in the dark room.

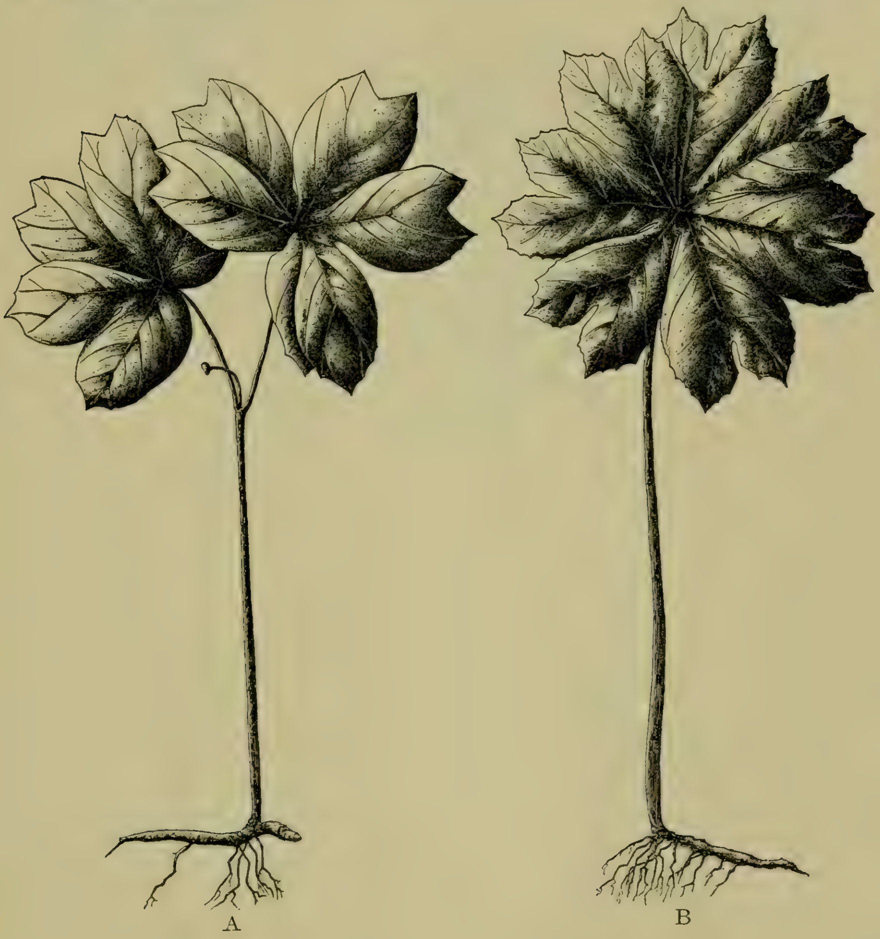

FIG. 110. *Podophyllum peltatum. A*, stem bearing flowers and two leaves; *B*, peltate leaf. Normal.

Polystichum acrostichoides (Michx.) Schott.

Clumps of *Polystichum acrostichoides* were brought in from the open, and forced in the dark room in February at the New York Botanical Garden. The fronds soon developed long upright stipes along which were borne the pinnae tightly rolled in clumps. Much of the excessive elongation took place in the basal portion, which attained three times its normal length. The sporogenous tissues at the

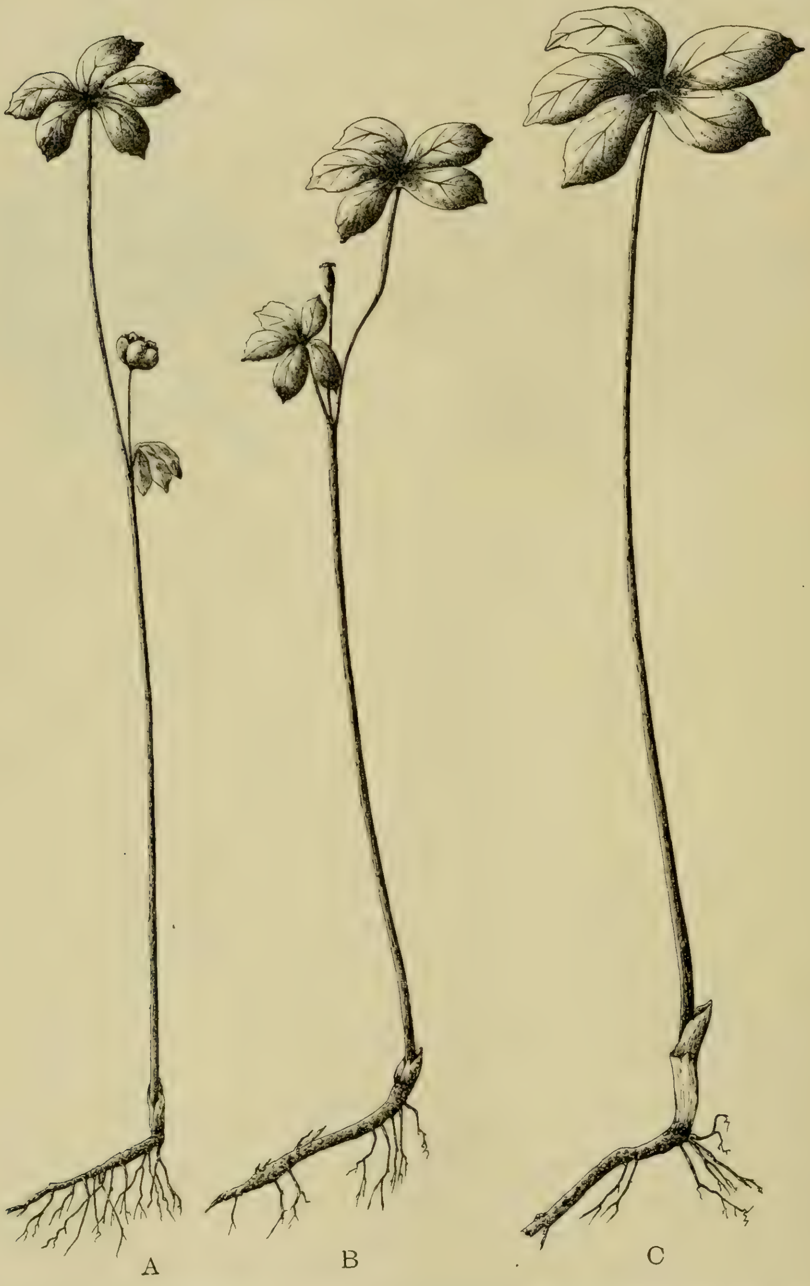

FIG. 111. *Podophyllum peltatum.* *A*, *B*, stems bearing flower and two leaves; *C*, peltate leaf. Etiolated.

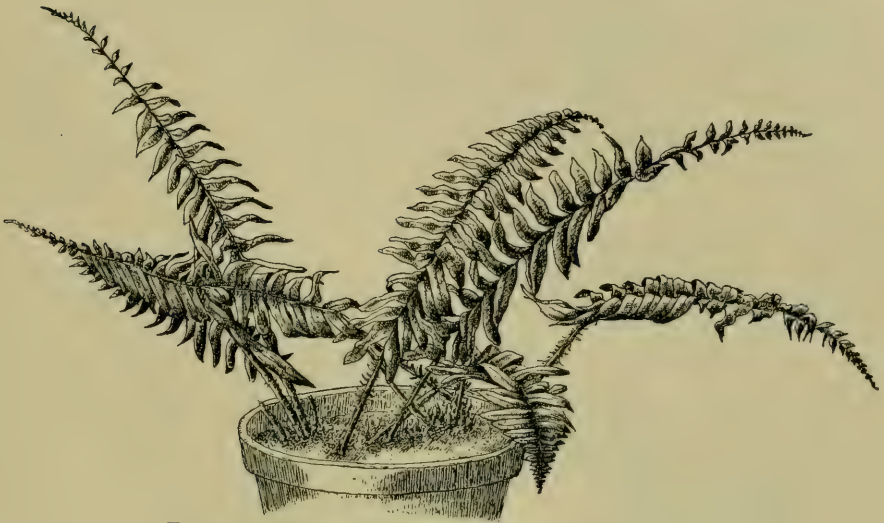

FIG. 112. *Polystichum acrostichoides.* Normal.

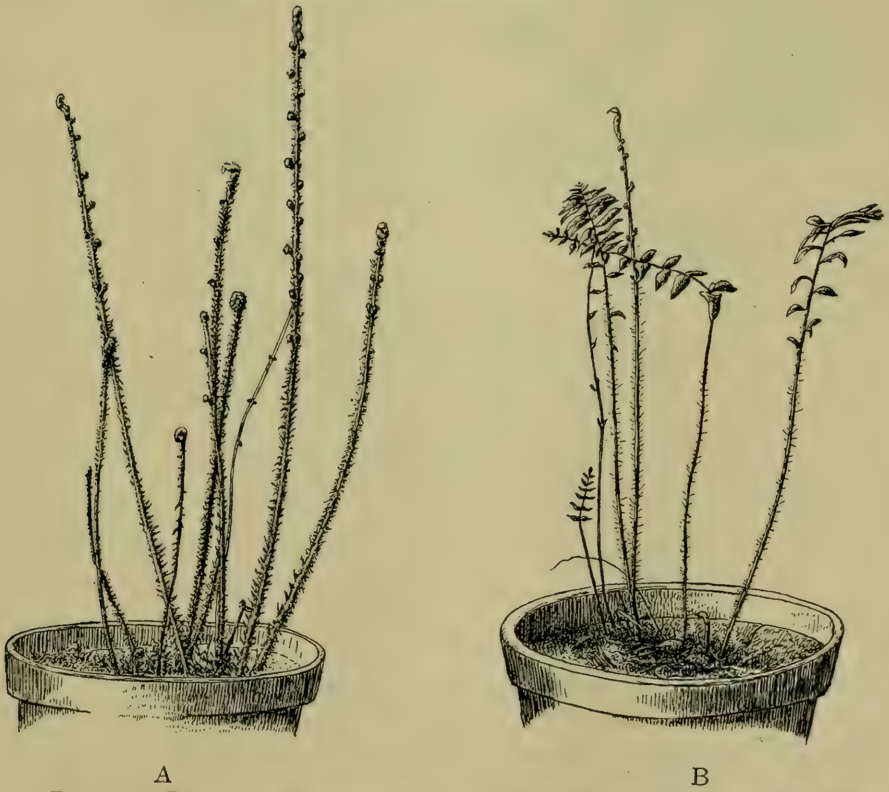

FIG. 113. *Polystichum acrostichoides.* *A*, etiolated culture. *B*, same after two weeks' exposure to illumination.

apical portion of the frond remained inactive. The other pinnae were curled with the lower outer surfaces outward.

Etiolated forms placed in light first assumed a position by which the terminal portion was carried more or less horizontal, and some expansion of the pinnae ensued, which however did not reach normal stature.

Populus Simonii Carr.

Some small trees of *Populus Simonii* 3 and 4 meters in height were brought into a cool house on December 1, 1901. Two weeks later several were removed to the control house and one to the dark room. Within a fortnight both showed signs of activity. The branches showed a tendency to develop the buds near the apex and base most strongly, the terminal bud making the greatest amount of elongation in both the normal and etiolated examples. A month after the beginning of growth the branches arising from the basal and middle regions of a normal branch showed 1–3 internodes with a total length of not more than 4 cm. The etiolated buds developed branches three or four times as long in similar regions, and the terminal etiolated buds developed branches with a length of 30 cm. or more, in some instances. The normal terminal bud sent out branches not more than 10 cm. in length, and with four internodes. The etiolated terminal branches showed eight internodes which were sometimes as much as 50 per cent. longer than the normal. Similar relations were found between the normal and etiolated branches over the entire plant.

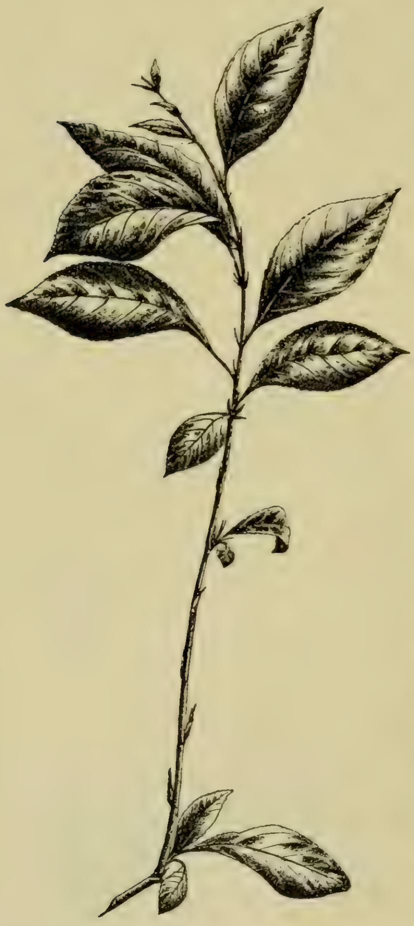

FIG. 114. Leafy branch of *Populus Simoni*. Normal.

The etiolated leaves were small, recurved with a petiolar portion a few millimeters in length, and the entire organ not more than 15 mm. long. The upper surfaces of the atrophied laminae were inrolled. The leaves were distinctly yellow while the stems were almost a pure white. The stipules were very nearly normal size in etiolated examples. A most striking phenomenon consisted in the

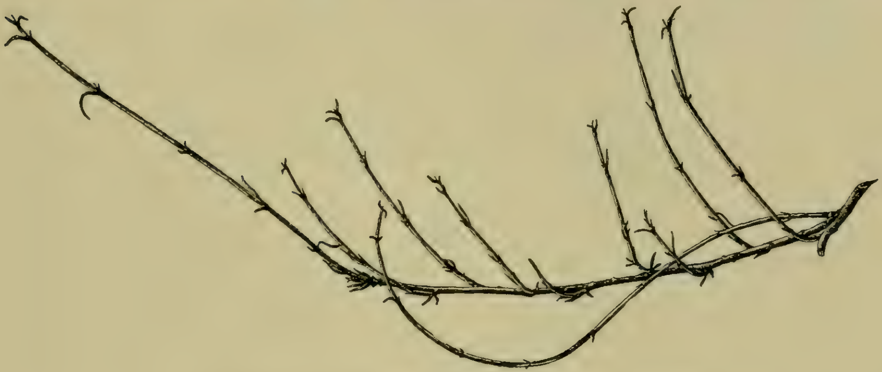

FIG. 115. Etiolated branch of *Populus Simonii.*

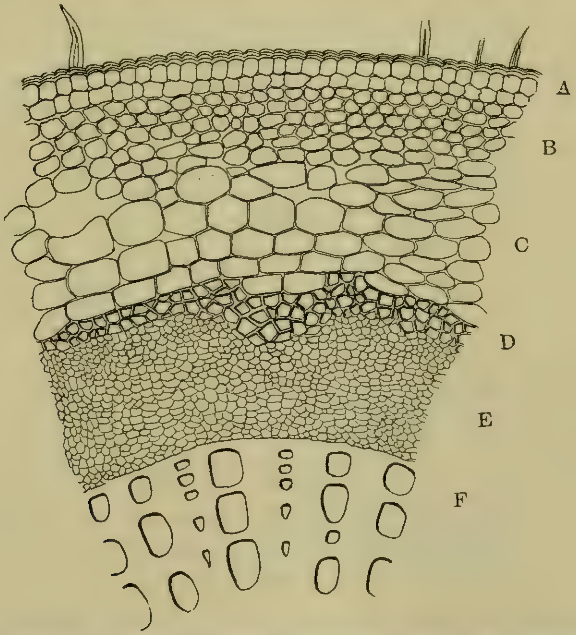

FIG. 116. *Populus Simonii.* Partial transverse section of normal branch. *A*, epidermis. *B*, collenchyma. *C*, cortex. *D*, bast fibers. *E*, cambium. *F*, wood.

superior thickness of the etiolated stems, which showed a diameter nearly 50 per cent. greater than the normal. This increase in size was accompanied by a loss of the winged angles characteristic of the branches during the first season of normal growth.

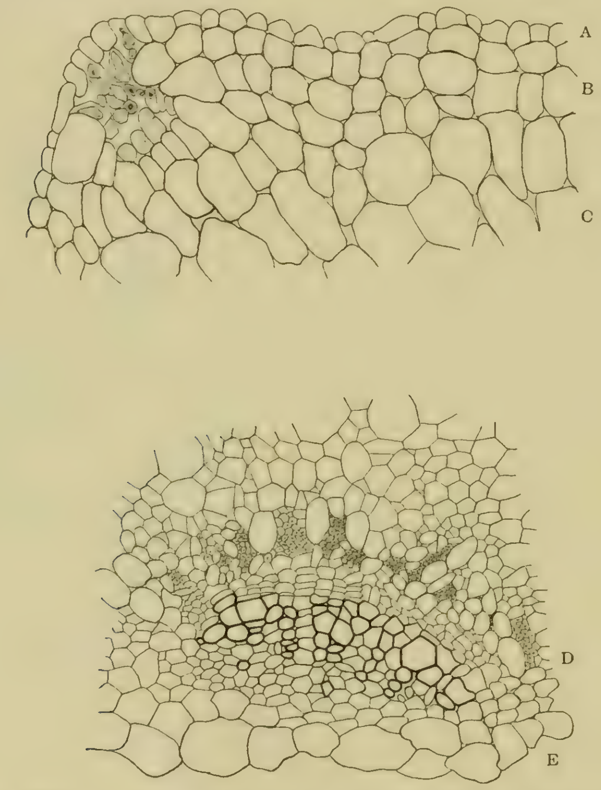

Fig. 117. Partial transverse sections of etiolated branch of *Populus Simonii*. *A*, epidermis. *B*, subepidermal region, showing earlier stages of a lenticel. *C*, cortex. *D*, bast fibers. *E*, cambium. (See Fig. 116.)

The epidermal and subepidermal layers lack the thickness of wall of the normal, and the hairs were scarcely half the usual size. Lenticels were to be seen in the earlier stages of formation on normal twigs, which were wholly lacking in the etiolated. The greater diameter of etiolated branches was due to the excessive development of the cortex, which was composed of larger elements with smaller intercellular spaces. The bast and sieve tissue as well as the cambium and xylem all showed arrested, or retarded development.

Potentilla sp.

Resting plants of a native species were brought in from the meadows in the autumn, and after several months in a cool dry room were placed in the dark chamber. The petioles developed a length of 14 cm., the laminar portion of the leaf being represented by a compact bud-like formation about 5 mm. long and 2 mm. thick. No other organs were visible and the limited activity of the leaves was coupled with a small supply of reserve material in the rootstocks.

Pteris longifolia L.

Clumps of rootstocks of *Pteris* were placed in the dark room early in March, 1901. In the succeeding cultural observations the fronds already formed persisted and appeared normal, the chlorophyl retaining its usual aspect. Young fronds sent up in the dark

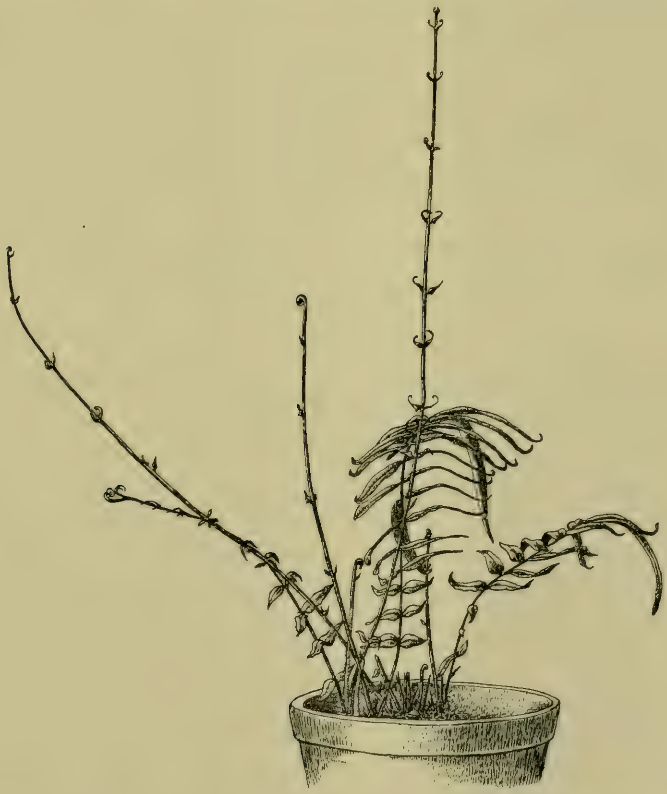

FIG. 118. Culture of *Pteris longifolia* with etiolated and normal leaves.

attained a length of 30 to 40 cm. The excessive elongation was shared by the entire stipe and midrib. The distance between the pinnae is 2 cm. normally, but in the etiolated it was 3 cm. The pinnae reached a length of about a centimeter, were curved and had the margins inrolled, and were about 3 or 4 mm. wide at the truncate cordate base. The entire frond contained chlorophyl, and the hairs were somewhat longer than in the normal examples. The number of hairs was about the same as in the normal, and the greater elongation of the frond made them appear more sparing, being distributed over a greater amount of space. Normal pinnae are about 6 to 8 cm. long and 1 cm. wide at the base. The transverse diameter of the basal portion of the etiolated stipes was about 2 mm. while that of the normal was 1 to 1.25. The increase was due chiefly to the increase in size of the fundamental parenchyma, epidermal and hypodermal tissues. Similar increase was also to be seen in the vessels. The frond actually unrolled its entire length in some specimens, the terminal lamina being borne on a stalk a centimeter long, and not attaining a length of a twentieth of the normal.

Quamasia. See **Camassia.**

Quercus palustris DuRoi.

Acorns of the swamp, or pin oak, of the crop of 1901 were placed in the soil in the control chamber and in the dark room in November, 1901, germinating in about four months. The normal seedlings had developed stems 2.5 to 3.5 mm. in diameter at base and about 25 to 35 cm. in length on July 6, 1902. The lower internodes varied greatly in length from a few millimeters to 5 cm. in one instance, and bore only small bract-like leaves. The terminal portions of the largest plantlet, about 3 cm. in length, bore 13 leaves, the uppermost of which approximated the adult type in size and form.

The oldest etiolated specimen had attained a length of 25 cm. and the internodes were more uniformly elongated to lengths of 1.5 to 3.5 cm., the length increasing as the tip of the stem was approached. A younger plantlet that had made more rapid growth had developed one internode 6 cm. long. The exaggeration in length of etiolated shoots of this species is clearly a matter of excessive elongation of the basal internodes, since the total number was much less than in the normal. The etiolated leaves were small and bract-like and the terminal portion of the stem was recurved, bearing the compact bud in a position favorable to piercing overlying layers of soil or humus. (See Fig. 119.)

The etiolated stems were not beyond 2 mm. in diameter in any instance, which was less than the normal. The reddish tinge of the etiolated stems was but little altered even in the oldest portions. The walls of the epidermal and underlying layers were slightly yellow, and indications of collapse were visible. No noticeable multiplication of the cortical elements could be detected. The formation of a phellogen in the medio-cortex had begun. The bast fibers were less thickened than in the normal, and were widely separated by the primary rays. The sieve cells were not distinguishable and cambium could be made out only in places. The xylem components were less highly developed than in the normal, and the walls of the vessels were comparatively thin. (Figs. 122–126.)

The basal portion of the oldest normal plantlets showed a distinct phellogen immediately underneath the epidermis and a loosely arranged cortex, in which no phellogen could be found. The cortex was richly loaded with chlorophyl. Numerous crystals in globular clusters were to be found which seemed wholly lacking from the etiolated.

Quercus rubra L.

Acorns of *Quercus rubra* were placed in the soil in November, 1901, in the dark room, and control chamber and germinated within a period of six months.

Normal plantlets on June 23, 1902, were from 8 to 15 cm. in height, with the internodes from 2 to 5 cm. long, inclusive of those of the terminal portion of the stem. The crowding of the leaves, owing to shortness of the uppermost internodes as in *Q. palustris*, was therefore lacking, but in several instances contiguous internodes were shortened in such manner as make it appear that the leaves were opposite or in whorls of three.

The basal portions of normal stems were about 4 mm. in diameter, tapering to half that amount at the tip. A few of the basal leaves were bract-like, but most of them were of the normal adult type, which, with the stems, were more or less pubescent.

Etiolated plants of the same age as those described above had attained a height of 30 to 35 cm., consisting of 10 to 12 internodes

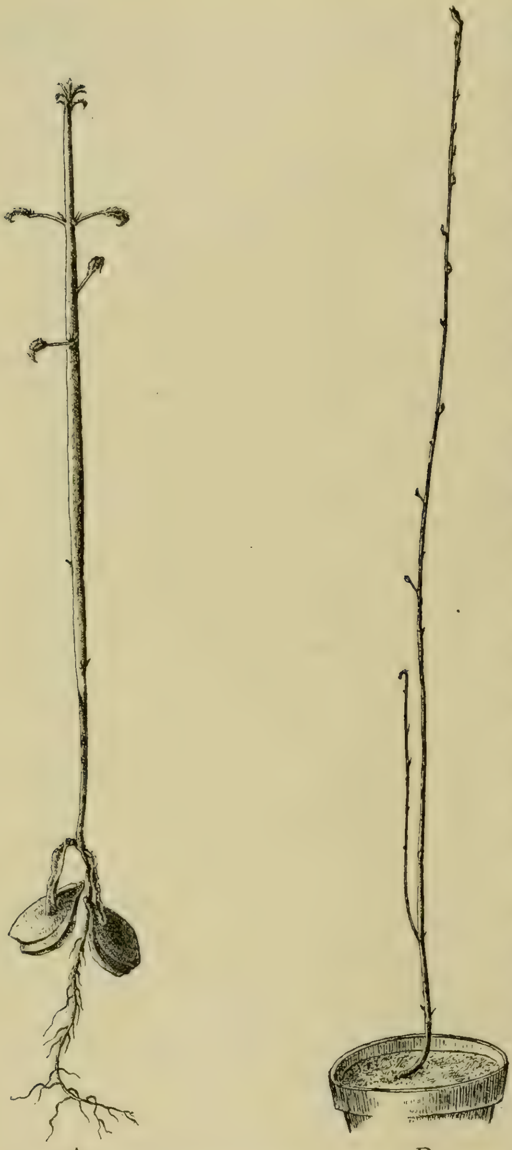

FIG. 119. *A*, *Quercus rubra*. Etiolated seedling with portions of acorn still adherent. *B*, etiolated seedling of *Quercus* sp.

and a sparse root-system. The maximum length of the internodes was about 5 cm., and the shorter ones were perhaps half that length, the whole stem showing a somewhat uniform excessive elongation of these organs, and in no instance were the leaves opposite or whorled. The leaves borne on the 8 or 10 lower internodes were small and bract-like, but those borne on the upper part of the shoot were of a general form similar to the normal, being about 1 cm. in length, the petiole occupying half that length. These organs were recurved with the apex of the lamina in contact with the base of the petiole. The curved and pointed hairs were longer than in the normal.

The basal portion of the etiolated plants had undergone discoloration of the epidermal and subepidermal tissues over a portion about 8 cm. in length. The maximum diameter of the etiolated stem was hardly greater than that of the normal in any instance. As in the other oaks examined, layers of phellogen were formed in the medio-cortex, while the external cortex and epidermis collapsed. The inner cortex was somewhat more compactly arranged than in the normal, and the lack of development of the stelar components was fairly similar to that described in other oaks. The normal stem has a subepidermal phellogen and a loosely arranged cortex containing much chlorophyl.

Quercus sp.

Germinating acorns of an undetermined species of oak were placed in the dark room in March, 1900. On May 19, cultures in the dark room showed stems with 30 internodes and a height of 75 cm., while the control plants in a room in which the temperature was somewhat more fluctuating and the air was dryer, showed 8 internodes and a length of 22 cm. Etiolated leaves about 1 cm. in length which was twice that of the stipules, were to be seen, with a small lamina, which was not entirely unfolded. The base of the etiolated stem had blackened and discolored up to a distance of 20 cm. from the base. A branch arose from the axil of the sixth leaf, and reached a length of 20 cm., bearing only scale-like leaves. The maximum length was shown by the fourth internode

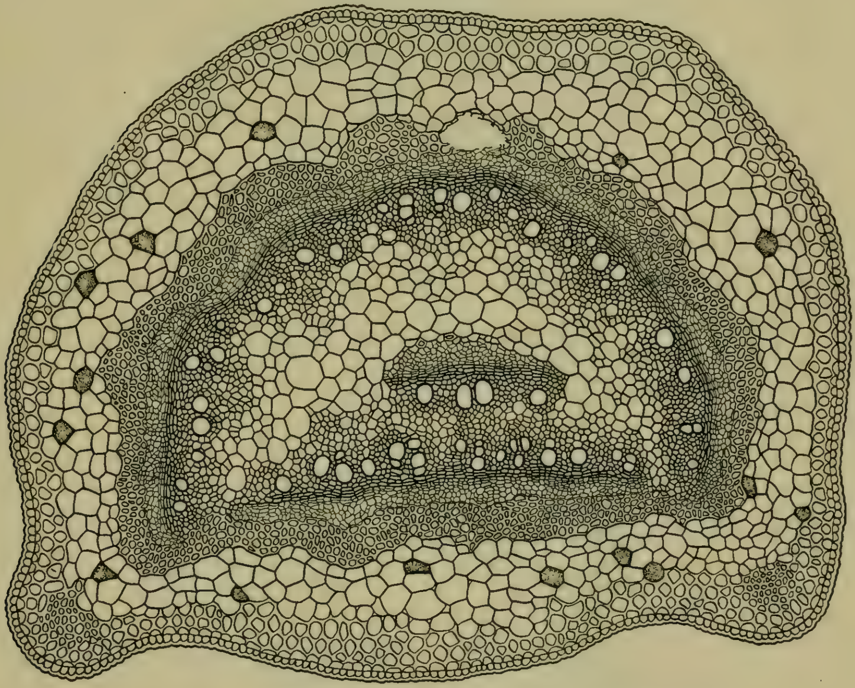

FIG. 120. *Quercus* sp. Transverse section of normal petiole.

from the base and by the basal portion of the branch. The greatest length of an internode was 5 cm. as contrasted with 4 cm. in the normal. It is thus to be seen that the excessive elongation of the stem was due chiefly to the multiplication and development of the internodes. The stipules were excessively lengthened and were persistent.

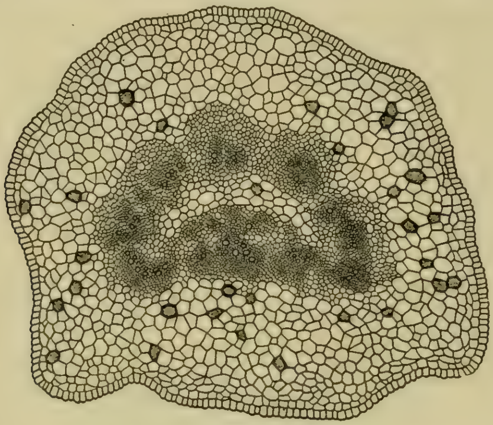

FIG. 121. *Quercus* sp. Transverse section of etiolated petiole.

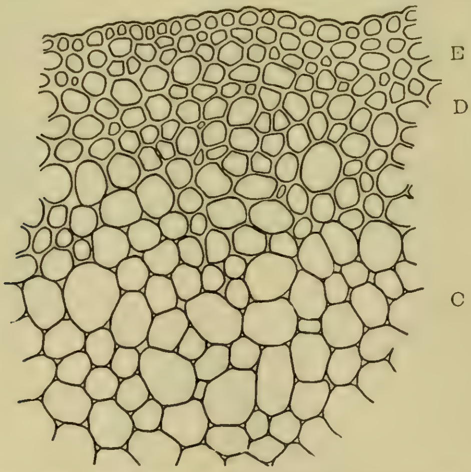

FIG. 122. *Quercus* sp. Partial transverse section of terminal portion of etiolated stem. *E*, epidermis. *D*, collenchyma. *C*, cortex.

The epidermis of the terminal portion of the stem was more or less thickened, and the hypodermal elements were also more collenchymatous than is shown by most etiolated forms. No differentia-

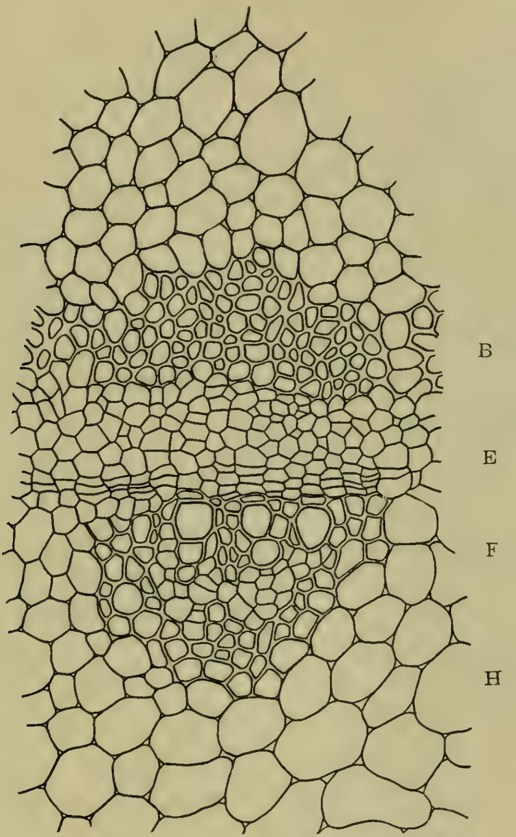

FIG. 123. *Quercus* sp. Partial transverse section of terminal portion of etiolated stem. *B*, bast fibers. *E*, cambium. *F*, xylem. *H*, perimedullary layer.

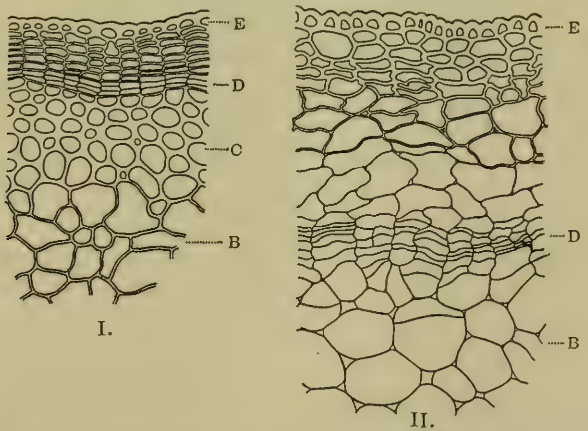

FIG. 124. *Quercus* sp. Partial transverse section of lower part of stem. I, normal. II, etiolated. *E*, epidermis. *D*, phellogen. *C*, collenchyma. *B*, cortex.

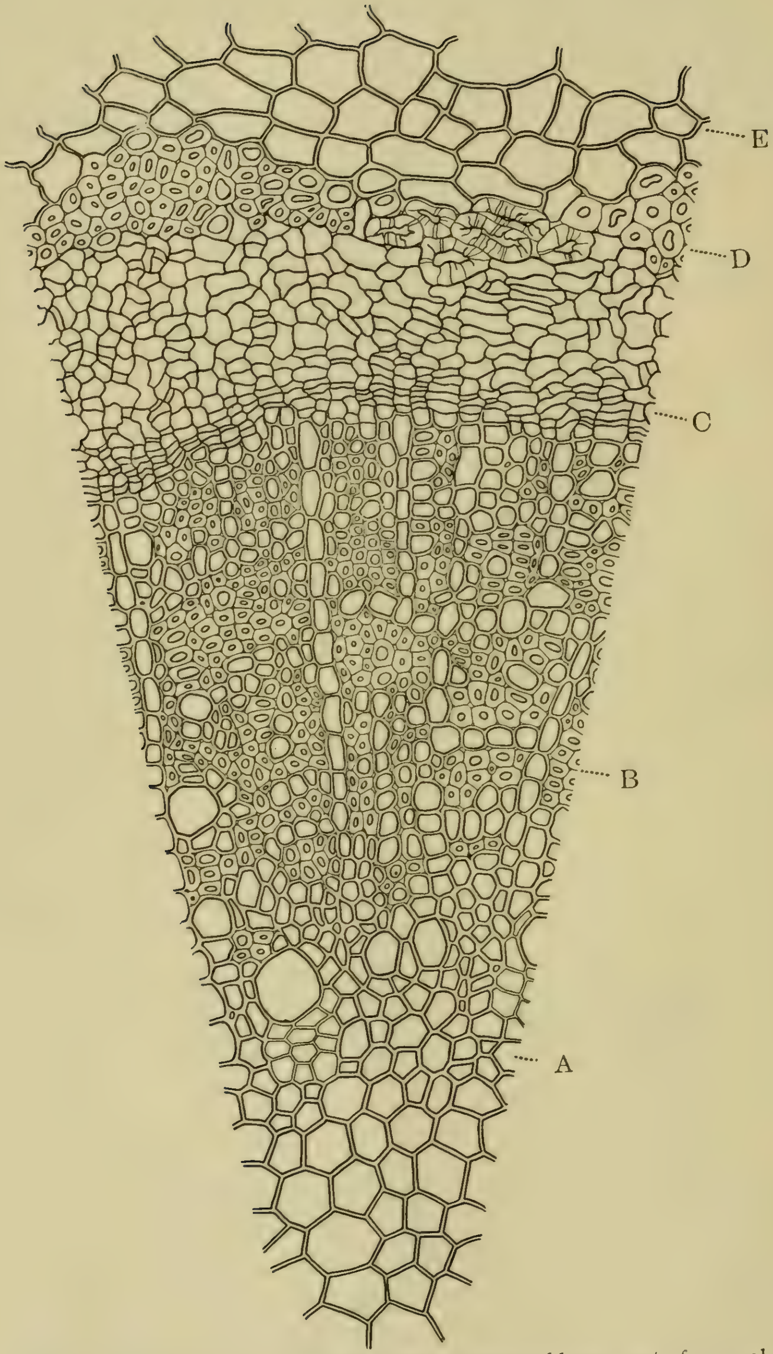

FIG. 125. *Quercus* sp. Partial transverse section of lower part of normal stem of seedling. *A*, perimedullary parenchyma. *B*, woody cylinder. *C*, cambium. *D*, bast fibers. *E*, inner cortex.

(p 164.)

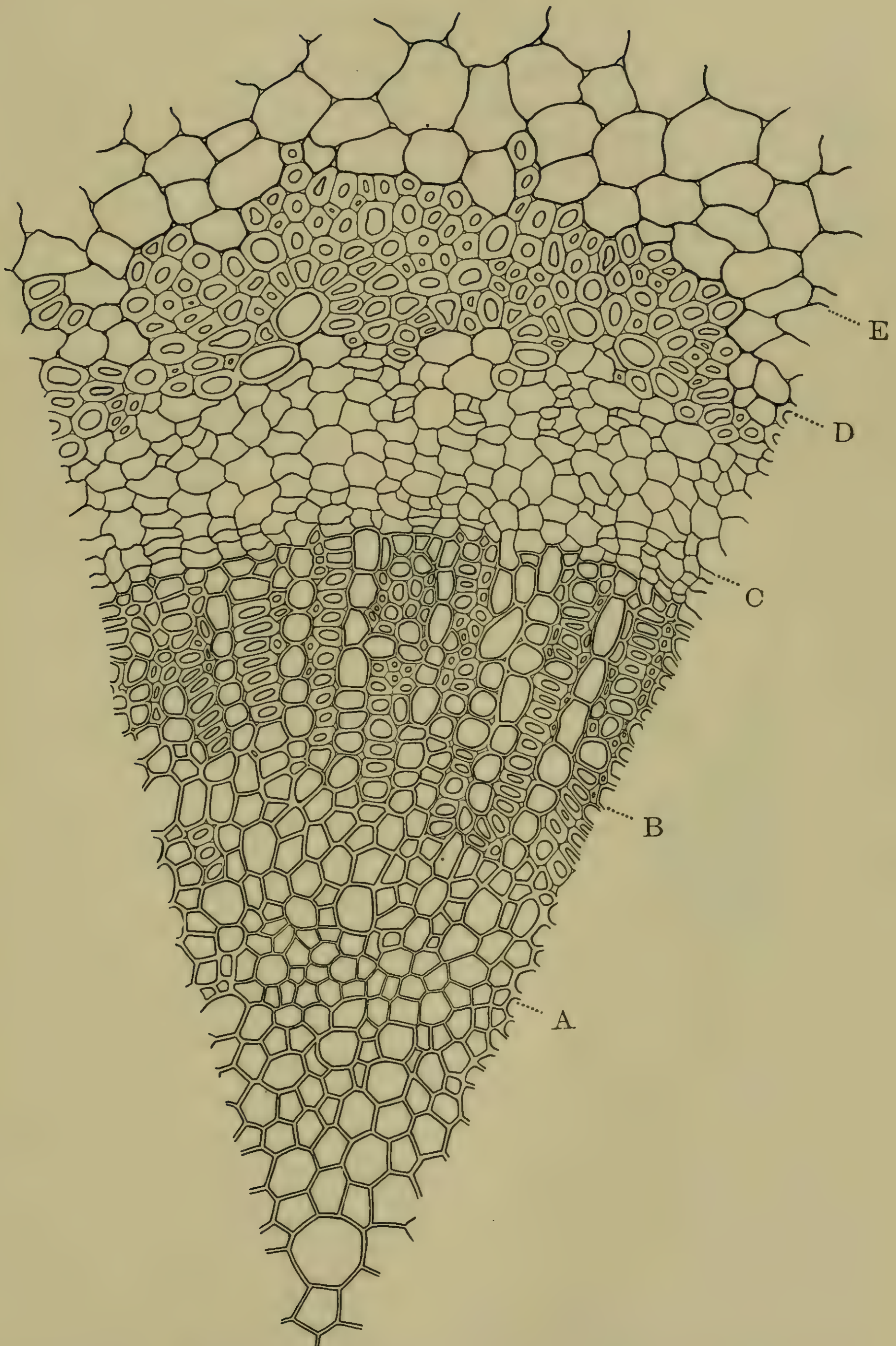

FIG. 126. *Quercus* sp. Partial transverse section of lower part of etiolated stem of seedling. *A*, perimedullary parenchyma. *B*, woody cylinder. *C*, cambium. *D*, bast fibers. *E*, inner cortex. (p. 165.)

tion of phellogen was found, although it was marked in the corresponding region of normal stems. The cortical cells in the etiolated appear to be smaller than in the normal stem, and more compactly arranged. The bast fibers form a continuous irregular circle in the cross section of the normal stem but were still separated by the medullary rays in the etiolated.

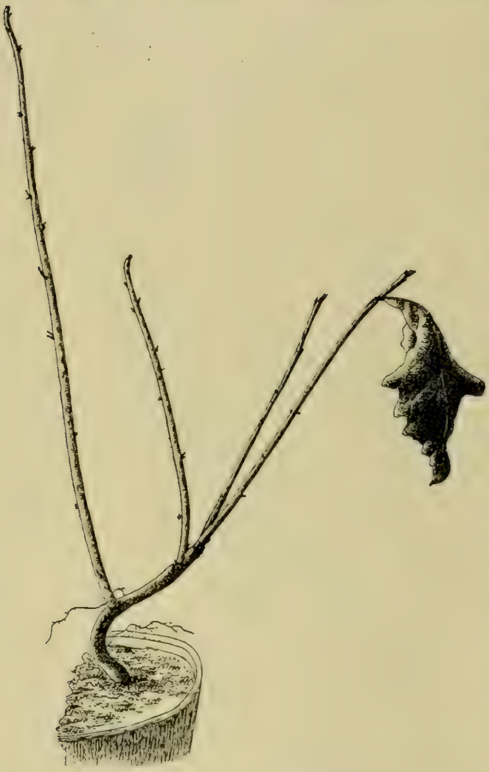

FIG. 127. *Quercus* sp. Seedling in second year. Normal (oblique) and etiolated branches.

The more interesting differences of structure were to be found in the lower and older parts of the stem. The epidermis and hypodermal cells in the etiolated had become irregular and were slightly collapsed. A phellogen had been formed in the medio-cortex, and the cortical cells were somewhat larger than in the normal, and with thinner walls. The difference between the bundles of bast fibers was still very marked. The sieve tissues showed a diameter about half that of the normal, and the cambium layer was not so well marked as in the normal. The elements of the xylem were in general larger in all dimensions, but the thickness of the xylem ring was hardly half that of the normal. The walls of all of the tissues in the xylem were thinner. (Figs. 123–126.)

The petioles showed corresponding differences in the normal and etiolated. The epidermal tissues were less thickened, and no collenchyma was to be seen. The separate bundles of the meristele were in a very rudimentary stage, with the sieve tissue but imperfectly developed, and the pericycle entirely lacking. The bundles were clearly separated by rays of parenchymatous tissue. (Fig. 121.)

A seedling of an unknown *Quercus* was brought into the dark

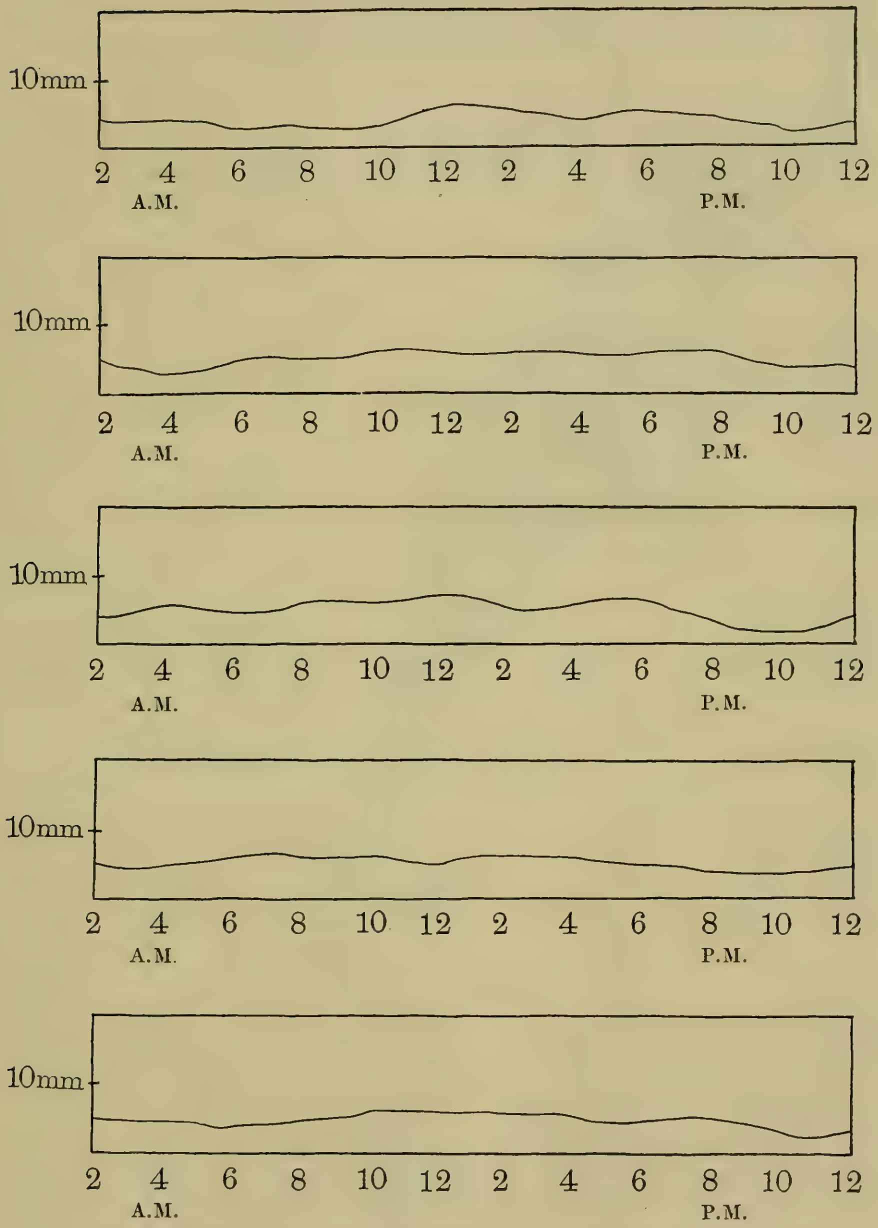

FIG. 128. Curve of growth of etiolated petiole of *Rheum* in dark chamber at temperatures 21–23°C. The actual amount of growth during the two hour periods is denoted by half the distance from the base line at a point above the numerals to the wavy line denoting rate of growth.

room in November, 1901. Two buds near the base of the young inclined stem soon awoke and formed stems 15 and 25 cm. in length. These etiolated stems were twice the thickness of the normal, due to the exaggerated development of the cortex and the internodes were longer than the normal. The leaves did not go beyond the stage described above. (Fig. 127.)

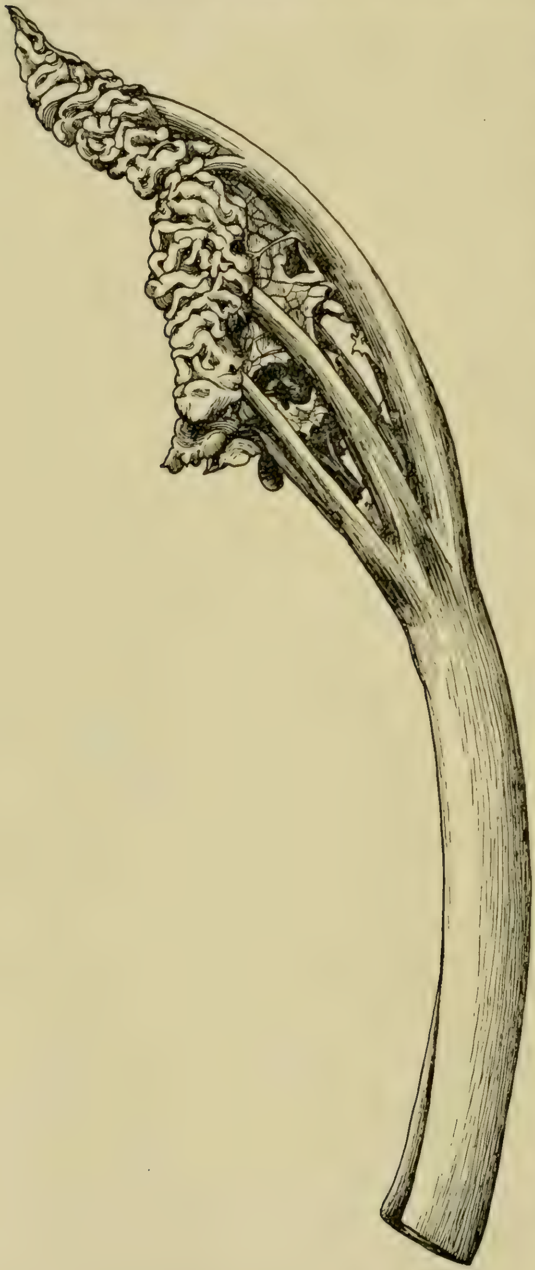

FIG. 129. Etiolated leaf of *Rheum*, ⅓ actual size.

Rheum sp.

Rootstocks of rhubarb obtained from a dealer were placed in a dark chamber in the early part of March and sent up leaves in which the petioles were both thicker and longer than the normal. The branches of the petiole in the laminar portion of the leaf separated but slightly, and in so doing ruptured the inactive lamina in many places, a phenomenon also observed in the related genus *Rumex*. Such etiolated leaves elongated at a fairly constant rate, the minimum being shown about 10 A.M. It could not be ascertained from the study of the auxanometric data whether this resulted from a true rhythm or whether it was the consequence of application of water about the hour in question, after which elongation increased. (Fig. 128.)

The composition of etiolated leaves of rhubarb has been the subject of many studies and tests on the part of practical investigators, and the cultivation of this plant in darkened cellars, and in total darkness is an industry followed by many gardeners. This method of cultivation appears to have been hit upon by Knight. A recent manual gives the details of management of these plants in darkness.[134]

Rhus sp. (native shrub).

A root of *Rhus* carried into the dark room in March with a clump of soil adherent had developed a shoot 35 cm. long with seventeen rudimentary leaves by May 1, the lower eight of which had fallen off. The angular outline of the normal stems was preserved, and a number of lenticels were formed near the base of the shoot. The pith was composed of uniformly thin-walled cells with large intercellular spaces. A cambium layer could not be made out, but some bundles which from their position must have been of secondary formation were to be seen. The cortex was very thin-walled and no thickening of the subepidermal tissues was seen. The epidermis was free from stomata, but bore numerous pointed and glandular hairs. The sections assumed a milky appearance on being placed in water.

The leaves attained a total length of over a centimeter and were curved downward. The two basal pairs of pinnae were extended but had a total length of only a few mm. The leaves were densely hairy, showing both forms of trichomes as noted below. No stomata were formed, which is correlated with the brief existence of the shoots which soon die in darkness.

Ricinus communis L.

Seeds placed in dark chamber germinated and produced hypocotyledonary stems 30 cm. in length, which were weakly erect. The cotyledonary stalks were 2 to 3 cm. long. The cotyledons were not freed from the endosperm in any instance, and made no growth, soon falling off, exposing the plumule. The first pair of leaves attained a length of about 8 mm. If the endosperm were removed the cotyledonary stalks curved downward after the customary move-

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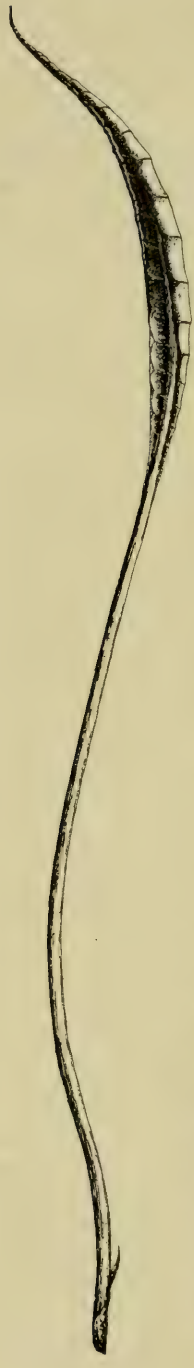
[134] Knight, T. A. On a method of forcing rhubarb in pots. Trans. Hort. Soc. Lond. 3: 154. 1820.

Morse, J. E. The New Rhubarb Culture. New York, 1901.



ment which brings the cotyledons to a horizontal position in normal plants.

In some instances the seedlings continued existence after the endosperm and cotyledons had been discarded altogether. The first internode often assumed a length of 5 cm. and had leaves with laminae a centimeter across, with the petioles reflexed.

Rumex sp.

A resting specimen of a *Rumex* native in the Garden was brought into the dark room December 1, 1901. Two weeks later the development of the leaves began and a succession of these organs were formed during the next four months. During my absence from the Garden during February and March, 1902, no observations were recorded, but 20 of these organs were seen and the plant was still alive and engaged in sending up leaves, on July 23, 1902, making an additional noteworthy example of a plant capable of extended endurance without the activity of the chlorophyl apparatus.

The petioles of the etiolated leaves attained a length of 30 to 35 cm. and were flattened on the inner, ventral surface. The laminae were represented by thin lamellae of yellowish tissue which extended along the midrib for a distance of 14 to 17 cm. with a width of about a centimeter narrowing toward the base and apex. The petiole appeared to be in a state of elongation throughout its entire length, and the excessive growth of its continuation in the midrib resulted in the rupture of the lamellar structures. In some instances the laminae showed sufficient resistance to set up a marked tension, by which the midrib was held in a curved position some time before giving way. The epidermal cells of the petiole were excessively elongated and some of the normal compound hairs were seen, being also present on the lamina. Perfect and functional

FIG. 130. Etiolated leaf of *Rumex* sp. ½ actual size.

stomata were found both on the petiole and laminae. Geotropic curvatures were exhibited by the terminal portions of some of the leaves which had fallen prostate while still growing actively.

Salvia sp.

Numbers of branches of a cultivated *Salvia* were thrust into small metal dark chambers during the course of the observations in 1896 and 1897. Such chambers were made as tight as possible by means of packing of cotton wool, but it can not be definitely affirmed that all light was excluded. If the branches had already laid down flower buds, a development would ensue in which the calyx would attain about two thirds of its normal size, but the corolla, which is usually much longer and highly colored, failed to emerge from the calyx, and was almost colorless. The stamens and pistils also failed to reach normal stature or to attain functional maturity.

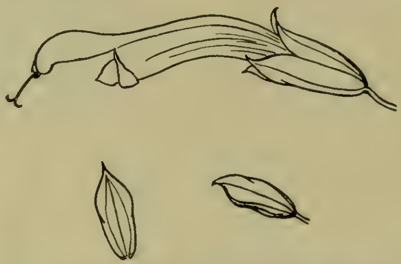


Fig. 131. *Salvia* sp. Normal flower with extended corolla and etiolated flowers with corollas atrophied.

Sansevieria Guineensis Willd.

A specimen was placed in the dark room in September, 1900, and when examined in May, 1901, nearly all of the mature green leaves originally borne by the plant were still alive and but little changed as to texture or color. Three young leaves which were about 10 to 15 cm. long at the beginning of the etiolation were now twice this length by basal growth, and the additional portion thus formed was a very pale green in color. One prominent terminal bud had become apogeotropic and formed an upright stem 15 cm. in height with the lower sheathing bracts about 12 mm. in length which is something in excess of the normal. This growth of the upright stalk was continued after a resting period in the summer of 1901 and in January, 1902, seventeen months after the beginning of the test, this stalk was 20 cm. long.

May 1, 1902, twenty months after confinement all of the leaves had perished, but the etiolated stalk still continued. The basal internodes had attained a length of 12 to 14 mm., but those nearer the tip

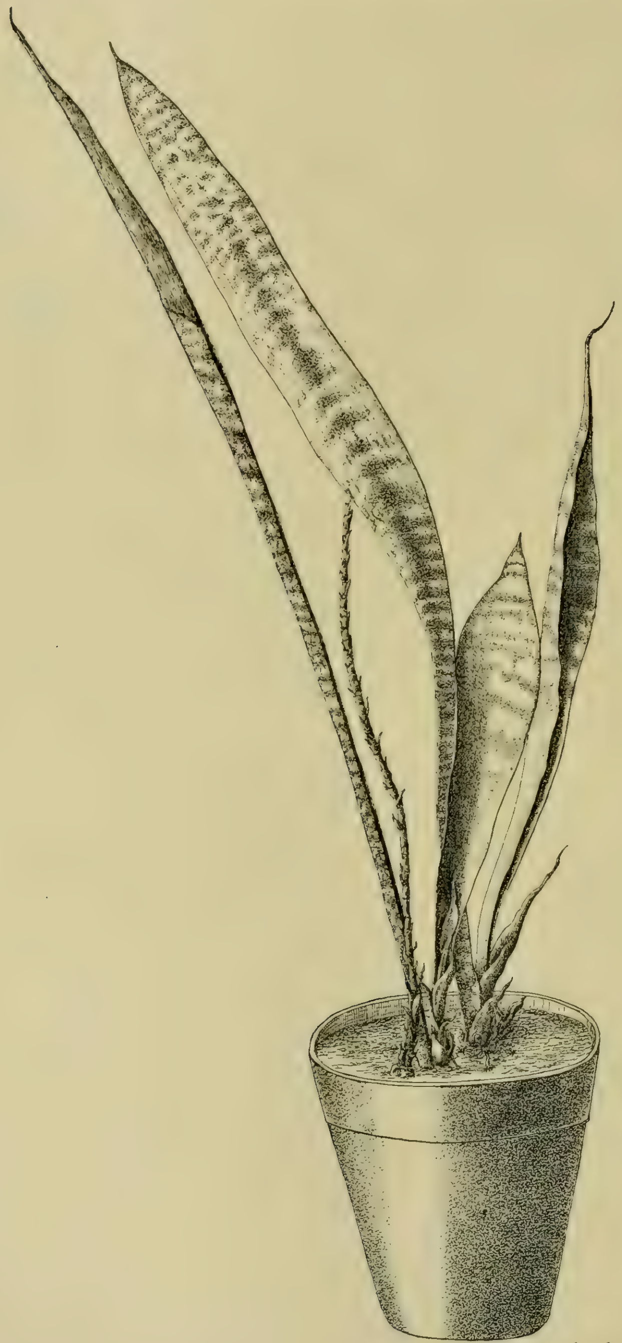


FIG. 132. *Sansevieria Suineensis.* Culture after confinement in dark room for 20 months

of the stem which had now reached a length of 35 cm. were not more than 5 to 7 mm. long. The stem had fallen prostrate by its own weight, but the terminal portion had curved upward apogeotropically. A number of small papillar projections a millimeter in diameter were seen emerging from various parts of the internodes. In some instances the emergences were from nodal areas, while in others a position in the middle of the internodes was occupied. Generally but one of these structures was found on each internode, but in some instances two were found. These emergences were supposedly young roots. The terminal half of this upright stem was imbedded in the soil in the propagating house, and developed a new plant, forming an exception to the old statement that etiolated organs could not be used as cuttings. The upright etiolated stem showed two or three layers of epidermal cells with brownish collapsing walls, a fundamental parenchyma of small elements, with some intercellular spaces. The outer fibrovascular bundles were notably reduced in both xylem and phloëm as well as in the stereome.

Sarracenia purpurea L.

Numbers of specimens were grown in the dark chamber in 1898. The leaves were wedge-shaped in transverse section, and slightly greater in diameter than the normal. The leaves already formed, and which had reached a length of a

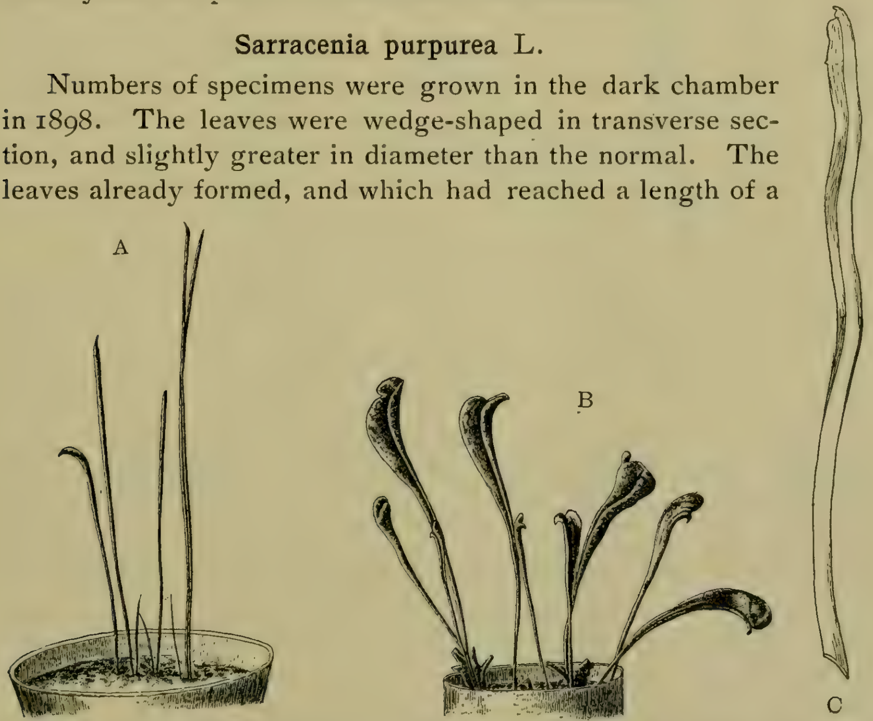


FIG. 133. *Sarracenia purpurea.* *A*, etiolated culture. *B*, etiolated culture after exposure to illumination for 18 days. *C*, etiolated leaf.

few cm. before being placed in the dark chamber formed a small pitchered cavity, and an extension of the flap to a width of 8 or 9 mm. The over-arching lip extended only 2 to 7 mm. beyond the end of the cylindrical portion which would have formed the pitcher in the normal.

Leaves which developed from the bud after being placed in darkness showed the normal size of cavity, but the lateral flap of the leaf was reduced to a wedge-shaped rudiment, and the arching lip was scarcely apparent. In such instances glands were found over the entire leaf and long, slender hairs were to be seen in the pitchered cavity. The diameter of the cavity in the normal pitcher was six to eight times that of the etiolated leaf. The etiolated leaf was twice as long as the normal, and much of the elongation took place in the basal

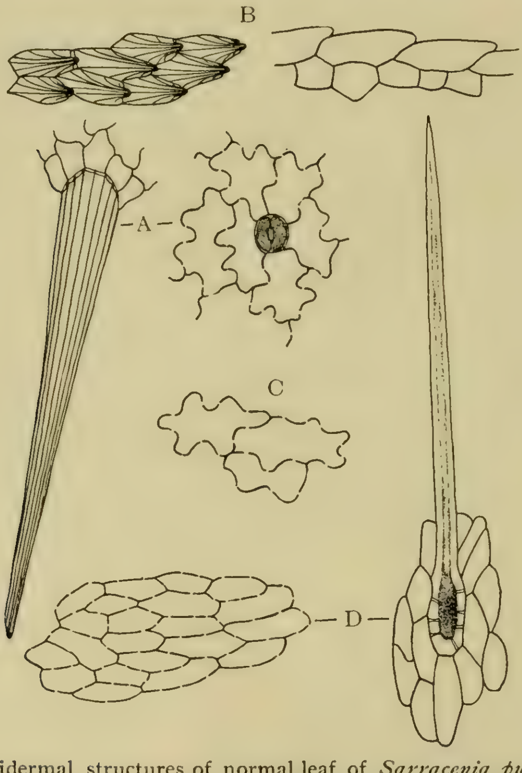


FIG. 134. Epidermal structures of normal leaf of *Sarracenia purpurea*. *A*, epidermal cell and hair from terminal flap. *B*, surface view and section of epidermis from "attractive" area. *C*, epidermis from "conducting" area. *D*, epidermal cells and hair from "detentive" region. After drawing Wm. B. Stewart.

portion of the leaf, which was five times the normal. This elongation also extends upward into the basal portion of the cavity of the pitcher which in the region below the detentive hairs was ten times the normal. The region covered by the detentive hairs was 1.4 times that of the normal. Above this the etiolated conductive surfaces was only one eighth of the normal and the attractive honey-bearing region had disappeared. The lateral flap of the normal was nine times as long and sixteen times as wide as the etiolated. The relative lengths of the various regions are shown in Fig. 136.

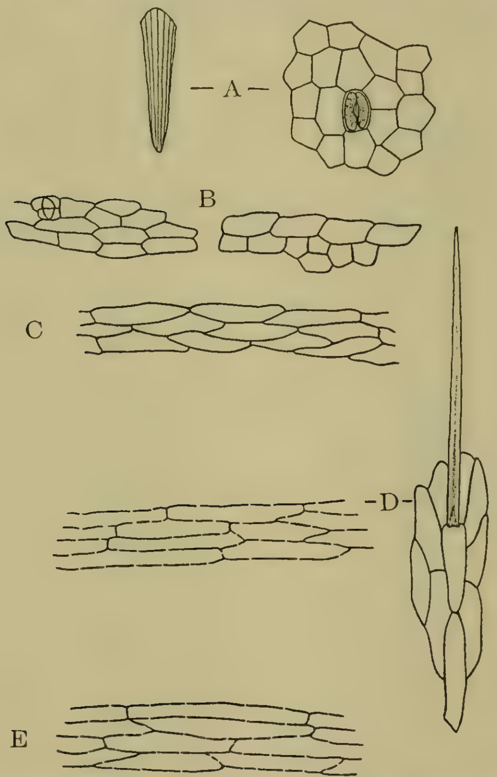


FIG. 135. Epidermal structures of etiolated leaf of *Sarracenia purpurea*. *A*, from terminal flap. *B*, "attractive" surface. *C*, from "conducting" surface. *D*, from "detentive" region. *E*, inner surface of cavity of ascidium. (After Stewart.)

The epidermal cells of the external surface of the upper part of the leaves ranged from 10 to 22 in length in the normal and from 25 to 63 in the etiolated. The width in the two instances ranged from 7 to 20 in the normal and from 3 to 5 in the etiolated. Not all of the stomata were differentiated.

The epidermal cells in the lower portion of the cavity which underwent excessive elongation were 1.64 times as long as the normal, but the normal were 1.4 times as wide as the etiolated. A similar relation holds in the detentive area where the epidermal cells were 1.29 times the normal in length but the latter are 1.55 times the etiolated cells in width. An increase of the actual number of cells in the etiolated detentive region was thus demonstrated. In the conducting surface the cells of the epidermis are 1.35 times the length of the etiolated, in the normal and are also 5 times the etiolated in width, showing a decrease in the number of cells. The same is true of the attractive surface in which the normal is more than twice the etiolated in all dimensions. Trichomes of all kinds are both longer and thicker in the normal.

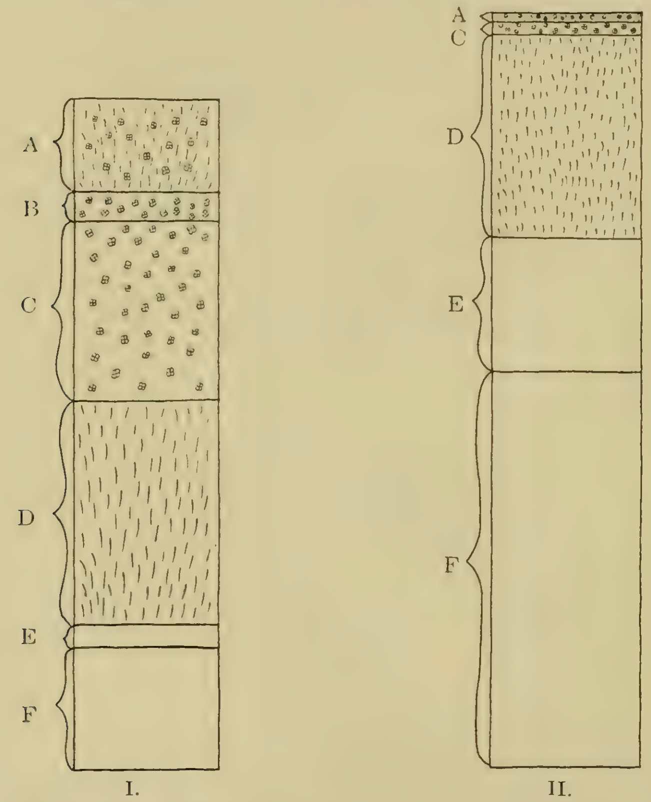


FIG. 136. Diagram showing relative development of various regions in normal and etiolated leaves. I, normal. II, etiolated. *A*. terminal flap. *B*, "attractive" surface- *C*, "conducting" surface. *D*, "detentive" surface. *E*, cavity below detentive sur. faces. *F*, petiole. Drawn by Wm. B. Stewart.

Sarracenia variolaris Michx.

Rootstocks of *Sarracenia variolaris* were placed in the dark room in January, 1900, and etiolated leaves had reached the maximum size

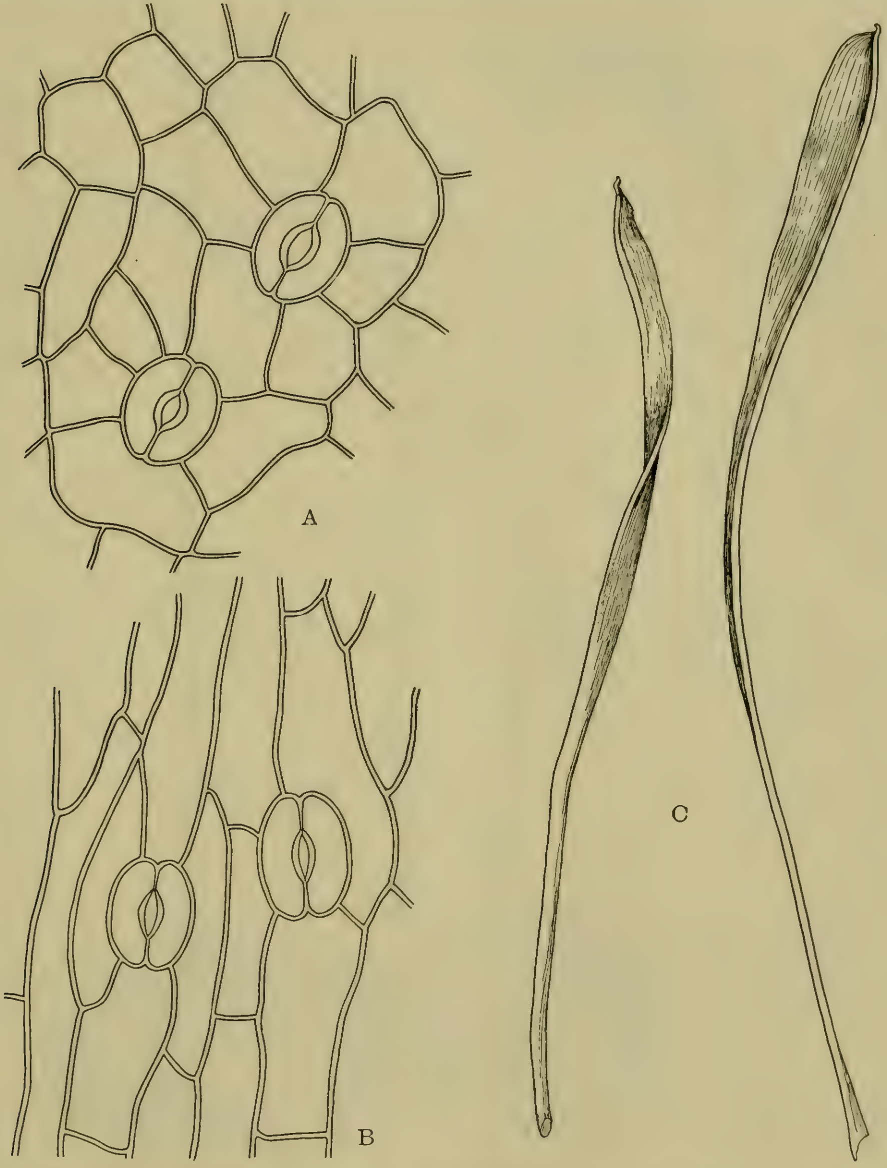


FIG. 137. *Sarracenia variolaris.* *A*, epidermis from outer surface of normal leaf. *B*, epidermis from outer surface of etiolated leaf. *C*, etiolated leaf.

in March. These leaves showed torsions of the basal portion, and attained a length of 18 to 20 cm., which was not in excess of the normal. The over-arching hood was found in the etiolated leaf as a conical pro-

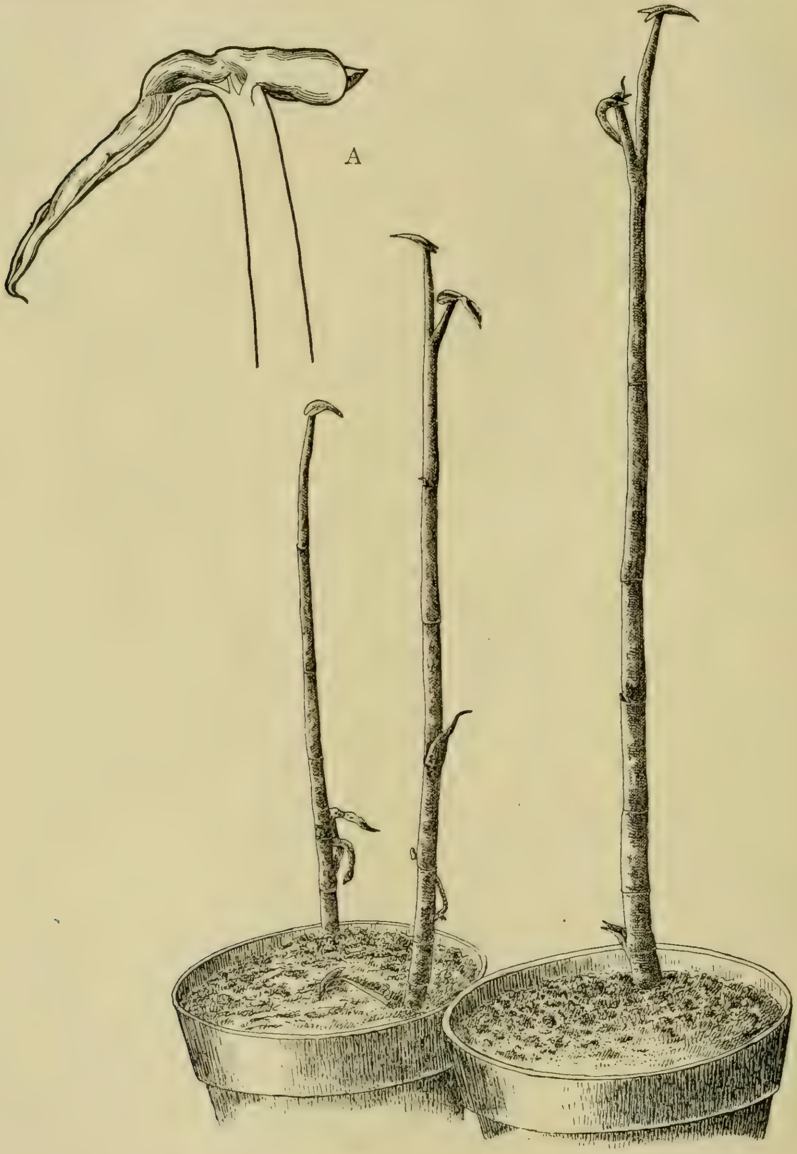


Fig. 138. Etiolated cultures of *Saururus cernuus*. *A*, lamina and portion of petiole of etiolated leaf.

jection 1 to 2 mm. in length, and generally two gland-like structures were to be seen on the upper edge of the lateral flap. Other rudimentary glands were to be found down along the edge of this lateral extension. The utricular cavity was present and extended to a depth of 3 to 5 mm. It was lined with small cells rich in protoplasm which were wholly undifferentiated. The epidermis of the outer surface of the leaf was composed of cells with four walls in surface view, and were also rich in protoplasm. Honey glands were present. The epidermal glands, as well as the stomata, were fairly normal. No trichomes were present. The pitchered cavity also lacked the hairs and glands of the normal. The leaves endured existence for three months after nearly full size had been reached. (Fig. 137.)

When etiolated leaves were placed in light the lateral flap underwent some extension but no great differentiation of the utricular formations ensued.

Saururus cernuus L.

Rhizomes placed in dark chamber in May, 1901, soon developed stems with a height of 40 to 54 cm., being composed of 9 or 10 internodes each 2 to 11 cm. long and showing a diameter at base of stem of 1.6 cm. and at apex of .6 m. The petioles attained a length of 5 cm. in some instances, but the sheathing bases did not keep pace

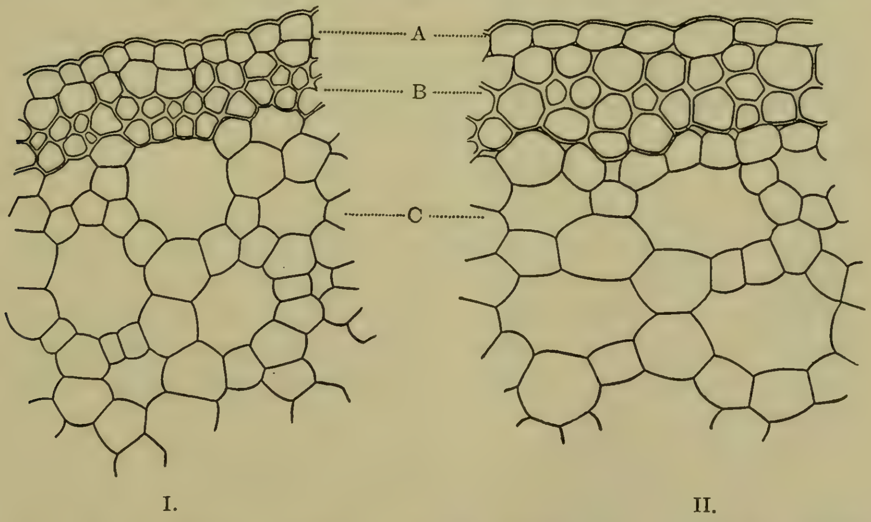


FIG. 139. *Saururus cernuus.* Partial transverse sections of etiolated and normal stems. I. Etiolated. II. Normal. *A*, epidermis. *B*, collenchyma. *C*, cortex.

with the thickening of the stem and they were soon cast off. The laminae were partially unfolded and measured about 5 by 3 cm. A few of the axillary buds showed some development and runners were sent out from the bases of some stems, each bearing several smaller leaves of the above aspect. It is to be noted that this plant roots in mud and may grow in water 60 cm. in depth. (Figs. 138–140.)

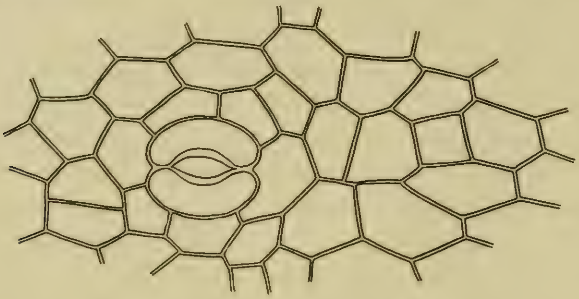


FIG. 140. Epidermis of etiolated petiole of *Saururus cernuus*.

Sparaxis sp.

Plants of *Sparaxis* placed in the dark room sent up leaves to a height of 10 to 20 cm. which were strictly erect and closely adherent, and soon perished. No flowers were developed. The humidity and temperature was probably too high for this species.

Solanum tuberosum L.

In tests to determine the length of time this species might endure continued deprivation of illumination it was found that two seasons might be passed without light, smaller tubers being formed on branches. The tubers formed during the second season perished because of unfavorable conditions in the culture room, and it is perhaps possible for this species to endure considerably longer periods without light.

A number of tubers were placed in the dark chamber in October, 1900, and by March, 1901, had produced a great number of lengthened club-shaped foreshoots which were 20 to 30 cm. long and 1.5 to 2 cm. in thickness with no geotropic sensibility. These stems were extremely brittle. Branches were curved in various ways and were easily detachable. Typical tubers were formed on the branches from such stems under the surface of soil. This experience was repeated in the winter of 1902. Similar shoots 60 cm. long were formed with but few branches. The epidermis formed a few functional stomata, and the epidermal cells contained highly granular lining layers of protoplasm. The thickened foreshoots described above grew and remained alive about six months.[135]

Taraxacum sp.

Rootstocks of dandelion placed in dark chamber showed some attenuation and a full blanching of the leaves. Excessive elongation ensued in the basal portion.

Tipularia unifolia (Muhl.) B.S.P.

Specimens received from South Carolina and placed in the dark room developed new corms of two internodes each 3.5 cm. long from the apical portion of which leaves 20 cm. in length were sent up. The laminae were rolled in a cylindrical form, and were wholly free from chlorophyl. The width of the leaves was about that of normal organs.

Trillium erythrocarpum Mx.

Corms placed in a small dark chamber in 1896 developed stems slightly longer than the normal with the leaves epinastic in such manner as to sheathe the flower bud. It is to be noted that these tests were imperfect etiolations. The flowers opened slightly, but did not form fruits (Fig. 141).

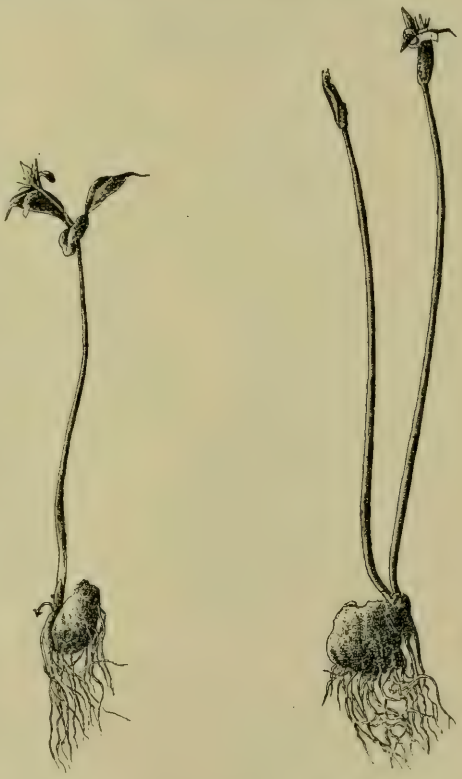


FIG. 141. Normal and etiolated cultures of *Trillium erythrocarpum.*

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[135] Batalin, A. Ueber die Wirkung des Lichtes auf das Gewebe einiger mono- und dicotyledonen Pflanzen. Bull. d. l. Acad. Imp. d. St. Petersbourg, 7 : 69. 1869.

In addition to other papers by Knight (see p. 4) and Vöchting (see p. 21), see Vöchting, H., Ueber die Keimung der Kartoffelknollen. Bot. Zeitung, 60 : 87–114. 1902.

Trillium erectum L.

Plants formed in the dark room in 1896 had the leaves appressed around the base of the peduncle and were smaller. The peduncles were not so long as in the average. The flower opened in a fairly normal manner, but did not produce fruits in these imperfect etiolations.

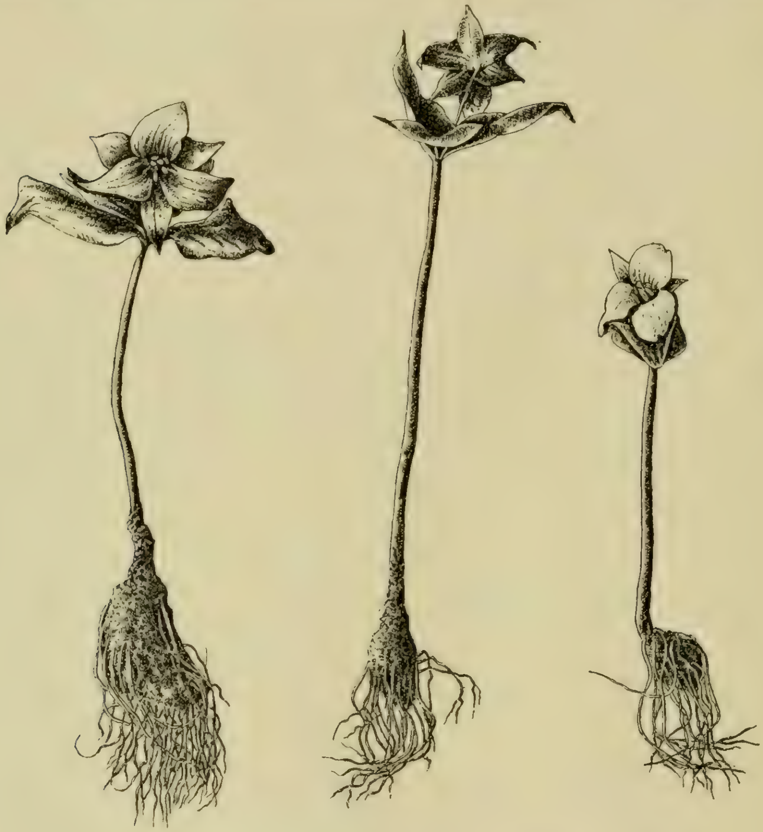

FIG. 142. Normal and etiolated cultures of *Trillium erectum*.

Milla uniflora R. Grah. = *Tritelia uniflora* Lindl.

Plants were etiolated in March, 1900. The leaves, which are normally twisted and curved, attained a length of two or three times the normal, being 35 to 50 cm. long and 5 to 7 mm. in width. Numbers of leaves from lateral buds attained a length of 10 cm. and a width of 1 to 2 mm.

The inflorescence axis emerged from the sheathing leaves at a distance of about 8 or 9 cm. from the bulb and was distinctly apogeotropic with the peduncles attaining a length of 14 to 18 cm. The flower stalks were extremely sensitive to light, soon showing apogeotropic curvatures. The etiolated flowers were enclosed by two translucent bracts united except at the tip and projecting beyond the flower 5 or 6 mm. These sheathing bracts arose about 5 or 6 mm. from the base of the flower tube. The separate portions of the perianth were about 16 mm. long, ovate and with the adnate stamens apparently perfect. The relative proportions of the stamens and pistils were as in the normal. (Fig. 144.)

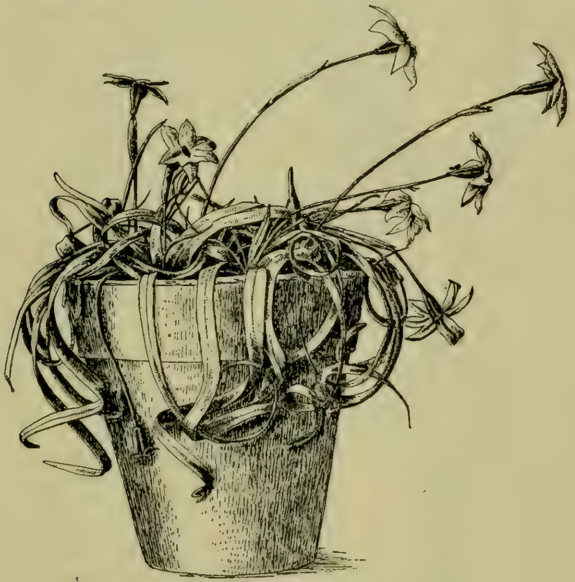

FIG. 143. Normal culture of *Milla uniflora.*

The normal leaf of *Tritelia* = *Milla* is 12 to 15 cm. long and 8 to 10 mm. wide, being perfectly plane in cross section, while the etiolated are crescentic. The flower and its stalk are about 18 cm. long and become negatively geotropic after fertilization. The sheathing bract is about 2.5 cm. long, splitting as in etiolated specimens and is dorsiventral. The ovary is about 2 cm. long and the perianth about 3 cm., being variously colored and marked with a purple midrib. The open perianth is wheel-shaped. (See Fig. 143.)

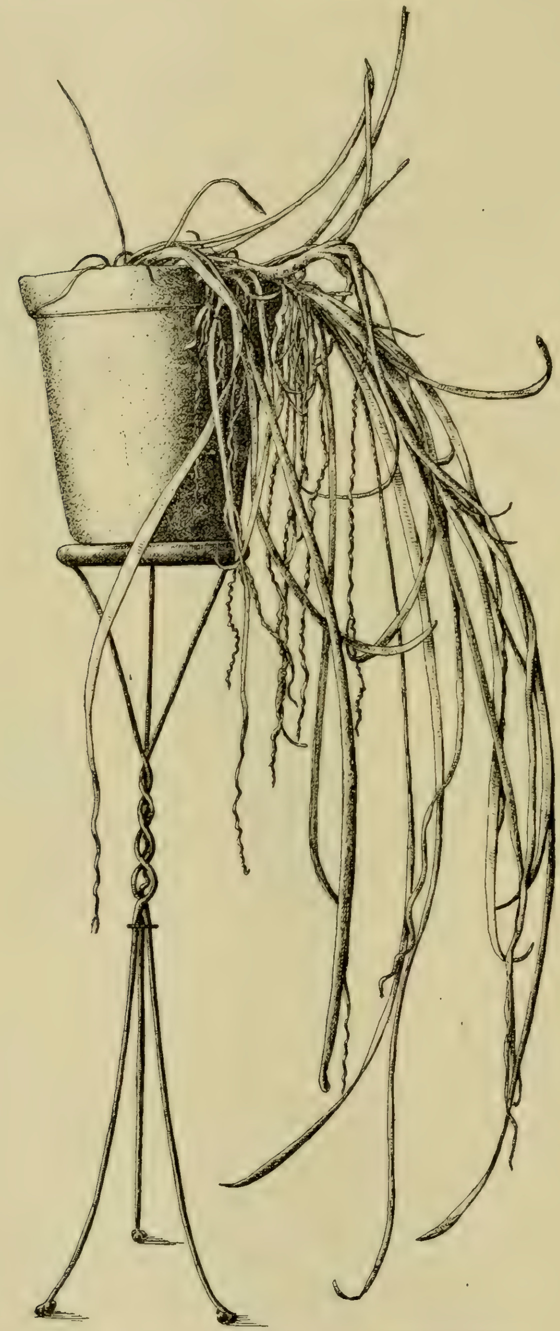

Fig. 144. Etiolated culture of *Milla uniflora*.

Tulipa patens Agardh.

Tulipa patens etiolated in spring of 1900, developed leaves 30 to 60 cm. long with inrolled margins and torsions present but not so marked as in *T. sylvestris*. The leaf from the lowest internode 7 cm. above the bulb was about 2 cm. wide at base and sheathed the second and third leaves. The second leaf arose from a node 4.5 cm. above the first and the third arose from a node 1 cm. above the second. The pedicel of the flower was about 6 to 8 cm. long, the perianth segments were 1 to 1.2 cm. long and were of a pale yellow. The stamens were of equal length and deep yellow. The pistil was about 1.4 times the length of the stamens. The pedicels reached a length of about 2 cm. and the floral organs slightly larger than the normal in some instances, being apparently perfect except for blanching.

Tulipa sylvestris L.

The leaves were 30–33 cm. long and trailing in etiolated specimens grown in 1900, and marked torsions were exhibited. The margins were tightly inrolled nearly half way to the center, and the entire blade was twisted tightly into a roll in which only the lower, outer surface was visible. The new bulb was formed laterally to the old one in a manner characteristic of the normal, both sending down long offsets. No flowers were developed.

Vagnera stellata (L.) Morong.

Etiolated specimens of *Vagnera stellata* grown in the dark chamber in April, 1900, showed a length of stem of about 55 cm. which was equal to that of the normal. The leaves were about 5 cm. long in the etiolated and 12 to 15 cm. in the normal. The upper part of the stem became horizontal in the normal, but remained upright in the etio-

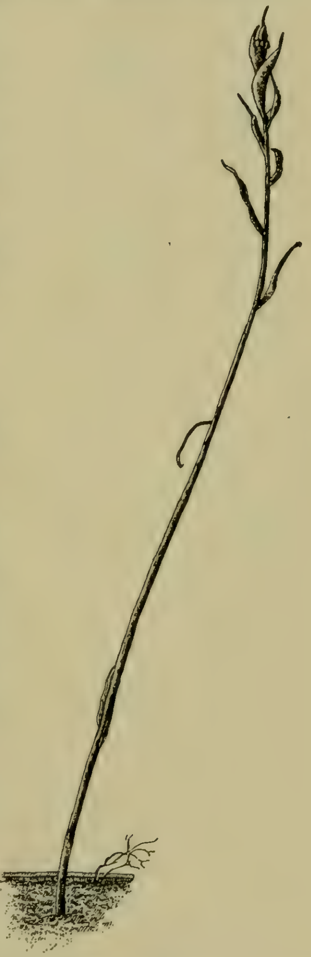

FIG. 145. Etiolated culture of *Vagnera stellata*.

lated. The leaves of the etiolated specimen soon perished, but the development of the inflorescence progressed so far that some of the terminal flowers had opened in a manner apparently normal.

The rootstock remained sound and healthy.

Viola obliqua Hill.

Specimens of a violet native to the Garden were taken from the soil in March, 1900. This is an acaulescent species which ordinarily sends only its petioles and peduncles above the soil. The petioles of the etiolated specimens attained a length about double that of the

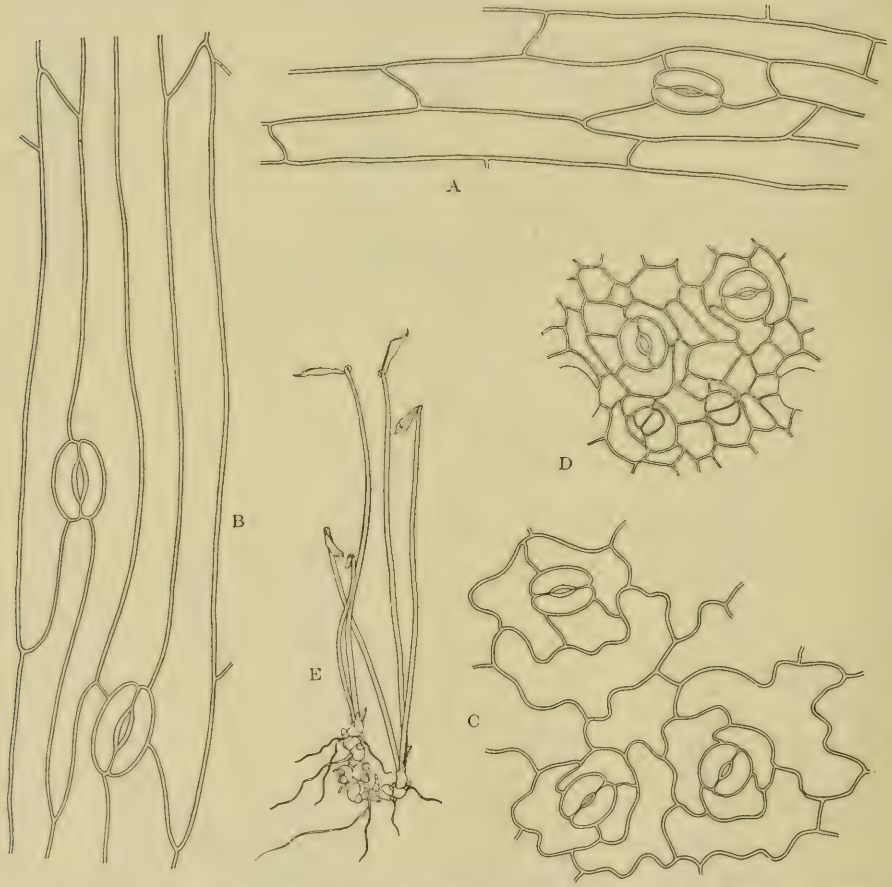

FIG. 146. *Viola obliqua*. *A*, epidermis of normal petiole. *B*, epidermis from etiolated petiole. *C*, epidermis from normal lamina. *D*, epidermis from etiolated lamina. *E*, etiolated specimen.

normal. The petiole at the base of the lamina was curved in such manner that the lamina was held pendant in an inverted position in the earlier stages of growth. With the growth of the petiole, this curve became accentuated until finally the tip of the lamina was projected upward, the petiole having curved through 360°. The epidermal cells of the etiolated petioles measured about 280 by 9, and of the normal about 65 by 9. The stomata were open and functionally normal. The thickness of etiolated and normal petioles was about the same. The laminae were rolled with the edges overlapping. Some of the stomata are functional but the greater number are not differentiated.

Viola rostrata Pursh.

Specimens of *Viola rostrata* were placed in the dark chamber in January, 1900. The shoot reached an extreme length of 18 cm. and the petioles of 6 to 10 cm. The laminae were not unrolled and were held pendant by a curvature of the petiole at the base of the lamina. In transverse section the epidermal cells were seen to be muriform and the middle of the laminae consists of four or five undifferentiated parenchyma cells with some air-spaces. The stomata did not open. The cross section of the petiole showed eight to ten fibrovascular bundles with annular, spiral and scalariform ducts present. The cortex was composed of twenty layers of large cells, equal to about half of the diameter of the pith. Small intercellular spaces were to be seen in the cortex. A subepidermal layer was slightly thickened. The epidermal cells were slightly papillose in places. No distinct cambium ring was formed. The stipules of etiolated specimens were about 4 by 7 mm., while in the normal they are but 3 by 1.5, thus showing an increase in size in darkness.

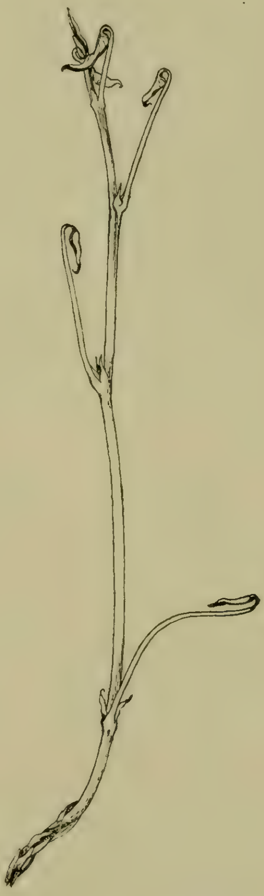

FIG. 147. *Viola rostrata*, etiolated shoot.

The normal stem had a cortex about equal to the pith in thickness and a heavy pericycle. A cambium layer was present in the normal. The subepidermal cells were well marked and large air spaces were to be seen between them and the epidermis. The development of the xylem scarcely exceeded that of the etiolated. (Fig. 147.)

Woodwardia radicans Sm.

Rootstocks of *Woodwardia* placed in the dark room in 1900 show a succession of stalks 25 to 30 cm. long and 3 to 4 mm. thick, bearing a few brownish scales which fell off later. The laminae and its branches remained as tightly rolled cylinders, which showed a distinct tinge of green, but which began to decay with no indications of opening. In its development it agreed fairly well with other Polypodiaceae.

The normal specimen has a leaf with a stalk 20 to 25 cm. long and passing into a rachis with a length at least 50 per cent. greater. The pinnae are widely spreading, are 20 to 30 cm. from tip to tip. The etiolated specimens therefore show only a development of the stalk perhaps slightly elongated beyond the normal, with the entire foliaceous portion inactive.

ADDITIONAL OBSERVATIONS.

Acer rubrum L.

A young tree of the red maple was brought into the dark room in November, 1901, and buds began to elongate on the lower part of the main stem early in the following May, followed later by the activity of others over various portions of the main stem and of the branches. The older etiolated stems reached a length of 15 to 65 cm. by July 22, and were about twice the thickness of normal twigs and shoots of the same tree formed during the previous season. Juvenile sprouts from the bases of young trees growing in the open, however, during the early summer, developed stems fairly equal to the etiolated ones, both in length and thickness. The etiolated stems were but weakly erect, soon falling over by their own weight whereupon the apical portions curved upward apogeotropically, giving the stems the appearance of trailing, and reminiscent of *Acer circinatum*. The normal branches of the tree in the dark room during the previous season in the open air, and of other trees in the open developed about 2 to 5 internodes of a thickness not more than one third of the etiolated, and a total length of not over 5 cm., the maximum length of single internodes being less than 5 cm. Etiolated branches developed 6 to 8 internodes, or about the same as juvenile sprouts, the maximum length of the internodes being about 14 cm., which was double that of the juvenile sprouts.

After the above growth had been made in darkness, the terminal buds perished, and activity was generally begun by the buds on the basal portion of the etiolated twigs, although some were developed on the terminal portions. It was noticeable that the greater number of buds on etiolated twigs that awakened were exposed to the occasional illumination of the gaslight by the aid of which examinations were made. In one instance an etiolated shoot showed a development of all of the main axillary buds on the illuminated side, and none on the other. The etiolated twigs bore pairs of opposite leaves, the petioles of which had a length of about 2.5 to 4 cm., and the small laminae measured 2 by 1.5 cm. being extended, and about one sixth of the normal size. (See Fig. 148.)

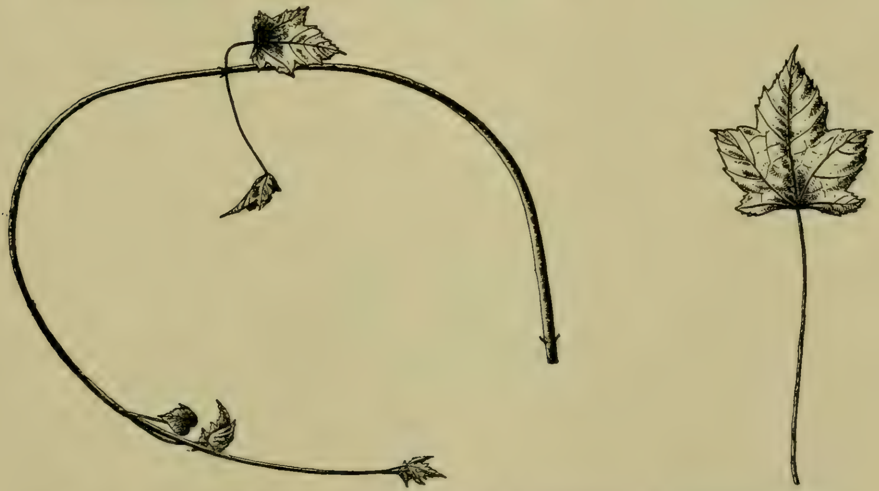

FIG. 148. *Acer rubrum*. *A*, etiolated branch with leaves. *B*, normal greenleaf.

The anatomical changes which may be ascribed to the effects of etiolation in *Acer* were more nearly parallel to *Cornus* than to *Quercus* or *Hicoria*. The subepidermal layers of cork were present, and the formation of lenticels had begun in the basal internodes of the etiolated stems. Such lenticels were larger and more numerous than in the stems of old trees in the open, but bore a general resemblance in occurrence and form to those on juvenile sprouts.

The walls of the epidermal and underlying tissues of etiolated twigs were slightly tinged with brown and the reddish cell contents of the normal epidermis were entirely lacking. The outline of the cross section of the normal twig is distinctly angular while in the juvenile and etiolated stems it was nearly circular. The subepidermal corky layers were present in the juvenile, adult and etiolated branches, the underlying cortex being thickened collenchymatously, pitted, and containing chlorophyl in the two normal forms, while in the etiolated the cortical cells were but slightly thickened, being flattened radially, with some intercellular spaces. The etiolated twigs showed, but a faint development of bast fibers, which with the lack of development of the collenchyma, must account for the mechanical weakness of such stems. The cambium layer is well marked in three kinds of branches, the wood cells and vessels showing larger lumina and thinner walls than the normal, although not so large as in the juvenile forms. The same may be said of the pith.

The epidermal cells of the normal twigs of juvenile, and adult sprouts and twigs show a length parallel to the long axis of the branch fairly equal to the width, being somewhat irregular in outline, while in etiolated examples these elements are drawn out into more nearly regular rectangles as seen in surface view, being about six times as long axially as tangentially. The tangential width of the epidermal cells was about the same as in normal adult branches.

The dorsal surfaces of the leaves showed stomata which were open when examined in water, and appear to be functionally active. The duration of the leaf did not exceed twenty days.

Trees beginning activity in the dark room in May, still bore etiolated shoots in various stages in the following September.

Jost cultivated some species of maple in the dark room in the winter of 1891 and 1892, and found that some of the buds of young trees developed into elongated etiolated shoots. The excess of growth in length was not so marked as in *Aesculus*, however. It was noted that some secondary thickening, or the formation of an additional ring of wood, was seen near the base of the etiolated shoot in the old stem.[136]

[136] Jost, L. Ueber Beziehungen zwischen der Blattentwickelung und der Gefässbildung in der Pflanze. Botan. Zeitung, 51: 108. 1893.

AEsculus Hippocastanum L.

Seeds of the horse chestnut placed in the soil germinated in the control chamber, and in the dark room in the following May. Normal seedlings sent up a stem in which only the basal internode developed a length of about 11 cm. and a diameter of about 9 mm. at the base tapering to 4 mm. at the summit. The normal seedling with a shoot consisting of a single internode on July 22, bore a single pair of quinate leaves and a strong terminal bud. The normal internode was somewhat angular in outline and of a deep green color. (See Fig. 149.)

On July 22 the single etiolated seedling on hand had developed a stem 50 cm. in length consisting of ten internodes, the terminal one of which had made about half of its probable ultimate growth. The basal internode was 12 cm. in length, and with a diameter of 7 mm., thus exceeding the normal slightly, both in length and thickness. This, as well as the other etiolated internodes, was compressed in the plane of the opposite leaves. The leaves were represented by pairs of sessile bracts with broad clasping bases and ciliate margins wholly unlike the foliar organs developed on the seedling. It is to be

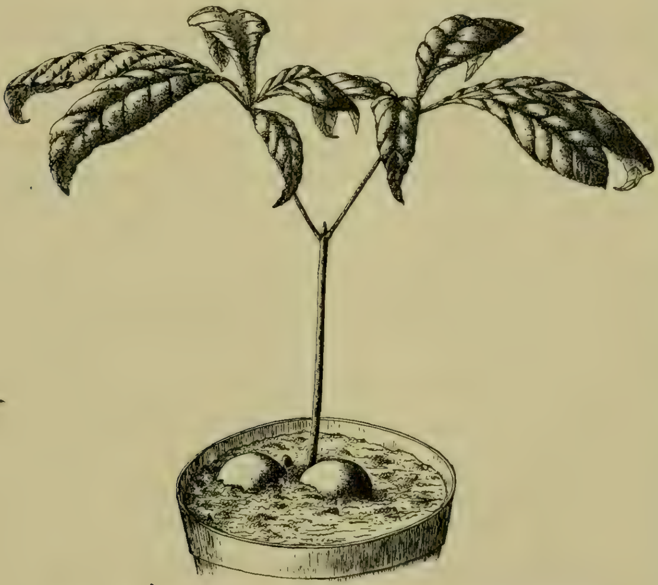

FIG. 149. *AEsculus Hippocastanum.* Normal seedling.

noted that the first pair of leaves in the seedling in this plant are truly foliar, and that these bract-like organs resemble nothing more than the cataphyllary leaves of the older stem. It seems probable that these bracts may be considered as the leaf-bases and they persist only a short time, being alive only on the second internode from the apex of the stem.

Numerous lenticels 1 to 3 mm. in length and half of that in width were to be seen, over the entire etiolated stem.

The epidermal cells of the etiolated stem had collapsed in the older portions, and were generally rectangular in surface view, being two or three times as long as broad. In some instances, however, the ends were acutely oblique. The phellogen underneath the epidermis comprised five to seven layers, and the outer cortex seven to nine layers, the latter being composed of elements heavily thickened collenchymatously, and flattened radially. The inner cortex was also similarly compressed, but the walls were not so heavily thickened. The bast fibers were only slightly thickened. Internally to these cells was found a mass of irregular thin-walled elements which shaded gradually into the cambium, which in turn passed gradually into the woody tissue. The vessels and tracheids showed larger lumina than in the normal. The pith was composed of perforate parenchyma richly loaded with starch, and it is to the exaggerated growth of this tissue that the excessive thickness of etiolated stems is to be ascribed.

The root system of the etiolated seedling was somewhat sparse, and the cotyledons were turgid and still contained some starch and other food material.

The normal stem of seedlings was furnished with a phellogen much like that of the etiolated, but the epidermal layer showed a number of outgrowths in the form of short-pointed hairs, which were not seen in the etiolated. The outer cortex is thickened collenchymatously, and contained much starch and chlorophyl, while the inner layer was composed of elements with much thinner walls.

The bast fibers were heavily thickened. The formation of some secondary tissue had begun on July 22, and the medullary rays were diverted from the radial position as if torsions had been set up. The outline of the stem was obtusely angular. The root system was more profusely branched than in the etiolated example.

A single seedling *AEsculus* was allowed to germinate in the control chamber in full illumination until the plumule of the young shoot was almost disengaged from between the cotyledons, and the curved portion of the stem already exposed bore a pair of small quinate leaves. The plantlet was then removed to the dark room and allowed to continue growth. Not only did the leaflets of the first pair of foliar organs continue growth, attaining nearly double the size shown at the time of their removal to the dark room, but all of the leaves borne on the etiolated and erect stem a month later also had five small leaflets which were entirely lacking from perfectly etiolated seedlings. It is thus to be seen that the stimulation of light upon the basal portion of the young shoot induced the development of laminar members on internodes which not only were not exposed directly to the light, but which were not developed until some time later. The evidence afforded by this demonstration also bears most strongly against the acceptance of any etiolation results in which light is excluded from a portion of the plant only.

Small trees of this species were cultivated by Bonnier in a continuous illumination from electric arcs of such intensity that oxygen was given off at one-third the normal rate by aquatic plants. Under such conditions the shoots did not attain normal size and elongated more slowly than under the usual conditions of alternating daylight and darkness. True foliar leaves were produced which were very green. No differentiation of bark or lenticels ensued, and the cortex was thinner than in the normal, as well as the central cylinder. The cortex was differentiated into two zones as it appeared to do under both normal conditions and in absolute darkness, in the experiments described above. The sinuosities of the pericycle were less accentuated. The thickening of the pericycle was less marked, and the woody tissue was less perfectly

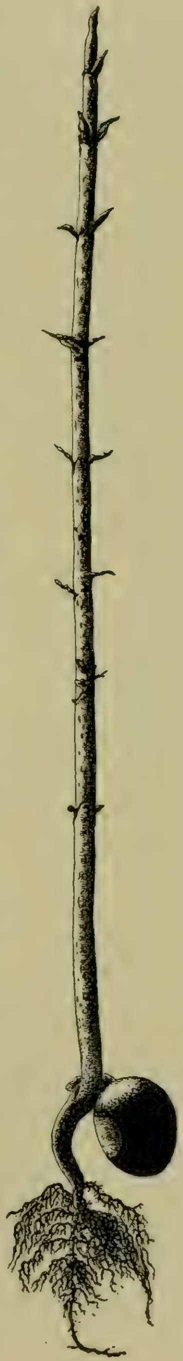

FIG. 150. *AEsculus Hippocastanum.* Etiolated seedling 60 days old.

developed. The greatest difference was to be seen in the secondary wood, which consisted of much smaller elements with thinner walls. The perimedullary layer was perfectly developed and the pith was greater than in the normal. The influence of weak continuous illumination is thus fairly similar to that of darkness, so far as the central cylinder is concerned. The differentiation of the cortical and epidermal systems is carried much farther in the etiolated specimen examined. It is to be recalled however, that Bonnier[137] used small trees showing adult stems, while the stem described above is that of the seedling, which in the normal, consisted of the first internode.

Apios Apios. (See page 42.)

After the first series of observations on *Apios* was made, opportunity was afforded for an examination of the subterranean branches upon which the tubers are formed by the swelling of the apical portions of the internodes. The earlier stages of the development of these formations was accompanied by the differentiation of a secondary cambium or generative layer in the pericycle, very similar to that exhibited by etiolated stems. The increase in the radial diameter of the cortex was not readily noticeable however in the tuber-forming stems. A subepidermal phellogen is formed early in the tuber-forming stem, but this does not take place in the etiolated, or in the normal aërial stem. Etiolated stems were free from trichomes, in contrast with the subterranean tuber-forming internodes, which bore these structures in great number.

Fagus Americana Sweet. (See page 105.)

Young beech trees from 30 cm. to 3 meters in height were brought into the control chamber and dark room in November, 1901. No activity was shown until July, 1902, when several buds on the smaller plants began to elongate, producing branches, which in some instances reached a length of 3 to 8 cm. by September 1, 1902. Such etiolated branches consisted of 3 to 6 internodes varying in length from 4 to 15 mm. and bore minute leaves on the basal portions and larger foliar organs on the terminal portions. The maximum size of these leaves was 8 cm. in width and 12 cm. in length. The leaves, as well as the stems, were silky-hairy, the trichomes having much the normal appearance.

[137] Bonnier, G. Influence de la lumière électrique continue sur la forme et la structure des plantes. Rev. Gen. d. Bot. 7 : 253, 254. 1895.

Buds were formed on the calluses over cut surfaces in a few of these small plants, and these, together with some of the awakening dormant buds, made a growth of a centimeter or less, then went into a resting condition being loosely covered with silky-hairy brown scales (see Fig. 152).

The above observations are fairly in accord with those made by Jost[138] upon *Fagus sylvatica* (?). Jost found that darkness hindered the development of beech buds, and that when a few buds were exposed to the light by the extrusion of a branch from the dark room, the others in darkness showed greater activity than the buds of plants wholly confined in darkness. The first crop of buds developed in darkness were but 3 cm. in length, and a second series awakening later made a growth of about 8 cm., bearing leaves about 5 cm. long. Jost believed to have demonstrated by his series of "partial etiolations" that some substance formed in light is necessary to the growth of buds of the beech.

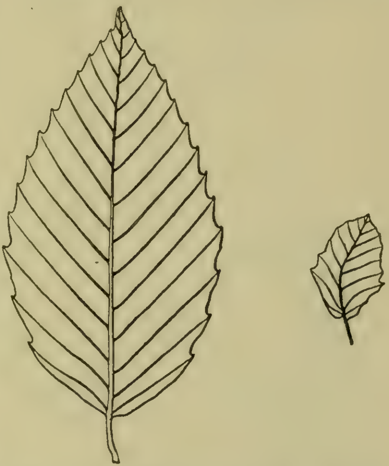

FIG. 151. *Fagus sylvatica*. *A*, normal leaf. *B*, etiolated leaf. Drawn to scale.

The larger trees used in my own experiments were trimmed by having a few of the larger branches cut away, and the only growth shown by such trees consisted in the formation of buds and branches from the calluses formed over the wounds. The buds in some instances did not elongate more than a centimeter before going into a resting condition, while in others branches 18 to 20 cm. long were formed, consisting of 5 or 6 internodes, of a length of 2 to 5 cm. and bore leaves which fell away after attaining a length of about 5 cm. The stems and leaves were silky with appressed hairs. Numerous lenticels were formed.

Normal stems of trees in the open air made a growth of 6 to 11 cm. in the season of 1902, and about 5 or 6 internodes were formed with lengths varying from 2 to 42 mm. The internodes of the

[138] Jost, L. Ueber den Einfluss des Lichtes auf das Knospentreiben der Rothbuche. Ber. d. Deut. Bot. Ges. **12**: 188. 1894.

etiolated branches are thus seen to be excessively elongated, a fact accounting for the superior length of these members.

The normal stem of the current season's growth showed a collapsing epidermis, an underlying collenchymatous layer of cortex, and an inner cortex with larger elements and thinner walls. Both regions contained chloroplasts. The bast fibers of the pericyclic region were grouped in such manner as to give the usual crescentic transverse section, being separated by the external continuation of the rays, which also separate the bundles widely. Some reddish coloring matter in the outer layer of the cortex was almost masked by the brownish tinge of the walls of the epidermis.

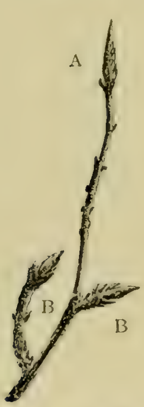

FIG. 152. Branch of *Fagus Americana*, which has been in dark room 8 months. *A*, normal bud which has not awakened; *B*, *B*, etiolated buds on short etiolated branches.

Etiolated stems showed structural divergences of degree only. The phellogen, collenchymatous layer and inner cortex were distinguishable. The cortical cells were furnished with thinner walls and contained so much reddish coloring matter that the etiolated stems had a decided pinkish tinge. The bast fibers, which are grouped in about twenty clusters in the normal, appeared in about forty smaller groups in etiolated stems, the crescentic outline of the transverse section appearing more flattened. The cause of this apparent multiplication of the clusters of bast fibers is not clear. It might be ascribed to the non-development of some of the fibers, thus breaking the normal clusters into smaller groups, the elements having thinner walls than in the normal. Cambium was present in etiolated stems and the medullary rays were not so wide as in the normal. Less thickening occurred in all of the woody tissues. Stomata were present on the dorsal (lower) surfaces of the etiolated leaves, although nothing but the most minute opening could be detected between the guard cells.

Bonnier[139] cultivated *Fagus sylvatica* in continuous illumination in the same manner as *AEsculus* (see page 191), and found that phellogen was not formed under such treatment. The number of sieve tubes was less than in the normal, and the rows of vessels and tracheids were seen to be more closely crowded together by the inferior development of the medullary and intravascular parenchyma as in etiolated stems of *F. Americana*.

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[139] Bonnier, G. Influence de la lumière électrique continue sur la forme et la structure des plantes. Rev. Gen. d. Bot. 7: 300. 1895.

Ibervillea Sonorae Greene.

A number of large woody tubers of "guarequi" were collected from the sandy plains around Torres, Sonora, Mexico, in February, 1902. Some were placed in the control house and others in the dark room in May, 1902.

Adventitious buds on the upper surfaces of the irregular tubers soon began activity, sending up vines 3 meters in height and climbing by means of extra-axillary tendrils after the manner of the Cucurbitaceae. These tendrils were extremely sensitive and reached a length of about 6 cm. The internodes of the glabrous normal stems were about 6 to 8 cm. in length, and the petioles about 4 or 5 cm.

Etiolated stems did not reach a length in excess of 50 cm., a limited growth perhaps partially due to the high humidity of the dark room. The plant is found to flourish best under the same conditions as subtropical cacti from the most arid regions of America. The internodes of the etiolated stems were fairly normal in length, except the basal ones which were much elongated, but were about double the thickness of green stems. Etiolated petioles were about a half longer than the normal. Tendrils were present, but did not attain the

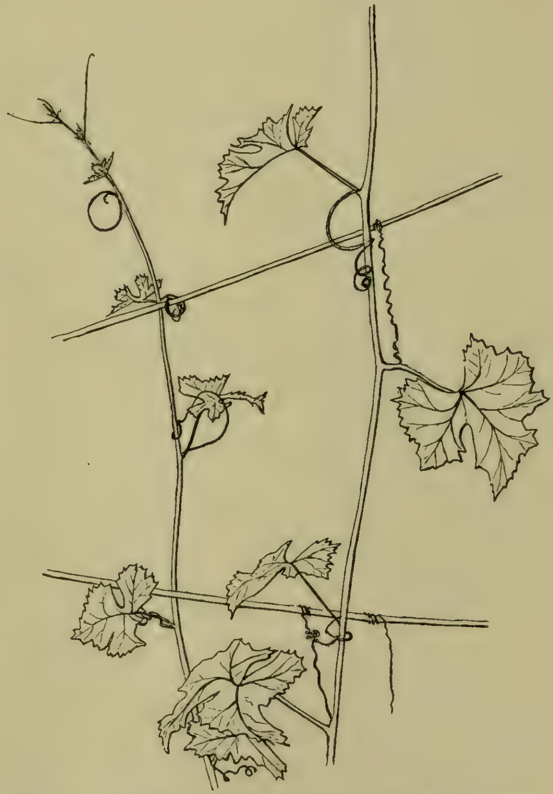

FIG. 153. Normal branches of *Ibervillea Sonorae.*

normal length, soon becoming curved as in normal mature organs, but did not assume the irregular corkscrew form of these organs. Etiolated tendrils were irritable to contact in the stage when they had reached a maximum size, but the resulting curvatures carried the tips through only a few degrees, except with continued contact, and in a few instance these organs succeeded in encircling a support. If the irritable surface was placed in contact with a support one or two turns would be made around it, but the free portion did not assume the corkscrew form. If stems which had begun growth in light were removed to the dark room the first etiolated tendrils developed subsequent to the removal were larger than if the entire growth had taken place in the dark room, affording another example of the endurance of the stimulating effects of light in partial etiolations.

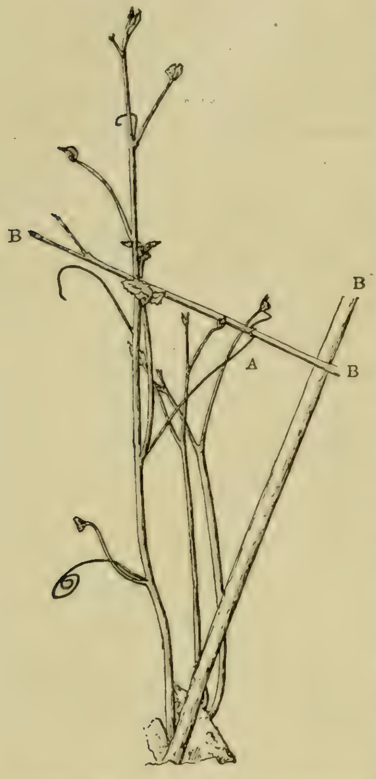

FIG. 154. Entire etiolated shoots of *Ibervillea Sonorae*. *B*, *B*, support, clasped by a tendril at *A*.

The excessive thickness of etiolated stems was found to be due to the greater size, and perhaps some multiplication, of the parenchymatous elements in the stele and cortex. The tips of the stems as well as the petioles were apogeotropic.

Lycopodium lucidulum Michx.

A number of bulblets of *Lycopodium lucidulum* in the germinating stage were found near Cold Spring Harbor, L. I., about the middle of July, 1902, and representatives of the various stages of development were preserved, while some in a resting condition were brought in and placed in the dark chamber. These structures are composed of several thickened fleshy leaves, and are formed in the axils of stem leaves, being in fact modified branches, and containing much chlorophyl. About a month after confinement in the dark room, the main axes of the gemmae began to elongate, and sent up stems about 15 mm. in height, which were fairly equal to that of normal specimens. The etiolated stems were almost devoid of color, but a faint greenish tinge was noticeable in the leaves. The cells were larger in all measurements and the stelar tissues less perfectly differentiated. The etiolated stems were slightly thicker than the normal, and bore about five leaves, which were appressed and much narrower and shorter than the normal, being bract-like. The distance between the leaves was greater than usual, correspondent to the internodal elongation of the higher plants. One or two roots had been formed by some gemmae, and the latter has begun to assume a yellowish aspect as if the chlorophyl were breaking up. The growth of the etiolated plants continued for five weeks from the time of germination.

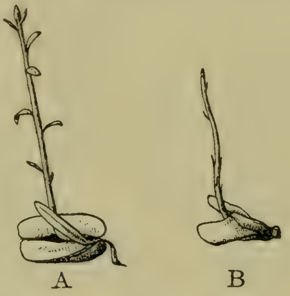

FIG. 155. *Lycopodium lucidulum.* *A*, normal plantlet arising from sprouting gemma; *B*, etiolated plantlet.

Smilax Beyrichii Kunth.

Tubers of *Smilax* from Florida collected in October, 1901, were placed in the dark room and control chamber in January, 1902, and began growth in May. On October 7, 1902, etiolated stems had been formed that had a length of 80 to 90 cm., consisting of 18 to 20 internodes of a length of 2.5 to 4.5 cm. Normal stems had formed a much larger number of internodes which made up a total length of 2 to 3 meters, the separate internodes measuring about double the etiolated members. Numbers of weak prickles half of the length and thickness of the normal were formed in darkness, in addition to which some papillar projections were formed on the basal etiolated internodes which were doubtless rudimentary roots. Leaves were represented on the etiolated shoots by sheathing bracts something larger than the normal, being over a centimeter in length, and bearing a narrow lanceolate body at the apex a few millimeters in length representing the petiole and lamina. Tapering papillae on either wing of the base near the lamina represented the tendrils. These organs arose from the extreme margin, and had the appearance both in the etiolated and normal organs of being branches of the hypopodium although designated as not homologous with any part of the leaf by Goebel.[140]

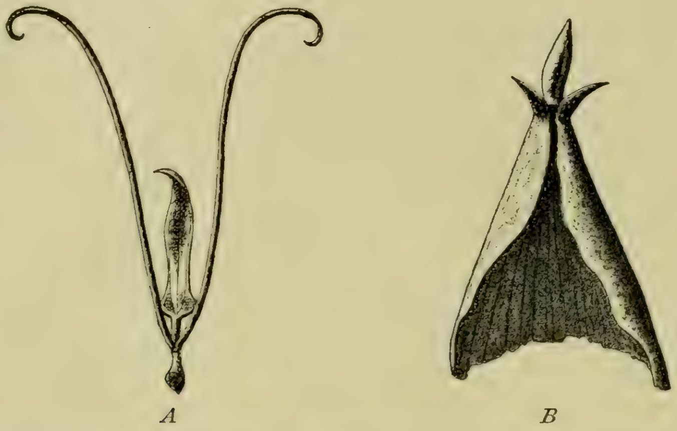

FIG. 156. *Smilax Beyrichii*. *A*, normal immature leaf with tendrils, natural ize. *B*, etiolated leaf, consisting of an exaggerated basal portion, bearing atrophied tendrils, and a rudimentary lamina, × 4.

Etiolated stems were thicker than the normal by reason of the increase in the size of the cortical cells, which were also furnished with thinner walls, the collenchymatous thickening to be found in the inner portion of this region in green stems being lacking. The numerous fibrovascular bundles were not so strongly developed as in the normal. The newly formed smaller bundles to be seen in the cortex of normal stems were not found in the etiolated stems.

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[140] Goebel, K. Organographie der Pflanzen. Part II., p. 432. 1898.

GENERAL CONSIDERATIONS.

Modes of Influence of Light upon Plants. — The relations in which plants stand to radiant energy are so diverse, and the several effects of light and darkness upon plants so intimately interlock that a brief statement of the currently accepted conclusions upon various phases of the subject will be a necessary preliminary to a critical discussion of the records of researches cited in this memoir, and of the new facts which have been brought out in my own investigations. The term light is used in the present paper to denote waves of radiant energy included in the spectrum between the infra-red rays with a wave length of $.760\ \mu$ and the supra-violet with a wave length of $.397\ \mu$.[141]

Sunlight has been found to exert analytic, synthetic, isomerismic, polymerismic and catalytic effects upon the chemical substances which may be isolated from the protoplasm of plants. It is fairly probable however that no such extensive action ensues when the various substances and compounds are bound up in the metabolic system of the living cell. At the present time evidence is at hand to show that certain synthetic effects, such as the union of oxygen with some portions of the protoplasmic substances, may be produced in the organism, and that it is to this cause that the destruction of bacteria in sunlight may be ascribed. It has also been found that light exerts a direct influence upon the enzymes in protoplasm. In the earlier stages of such action the effect of the red, orange and some blue rays seems to increase the amount of enzyme present, and later a disintegrating effect was exerted by these rays, the violet and ultra-violet being constant in such analytic or catalytic action. To the violet and blue-violet rays is also to be ascribed the oxidizing action noted above as well as the disintegration of chlorophyl. It is of course entirely probable that the action of light may set up chemical processes in the plant is in a manner entirely stimulative, and independent of any communication or transformation of energy. So far as known facts are concerned, the only method by which light might exert an effect upon growth would be by the decrease of the enzymes participating in the various stages of the process. That the rapidity of growth becomes less under illumination in many plants is beyond all doubt, but that such effect is due to the direct paratonic action of radiant energy is a matter that will come up for further discussion in this paper.[142] The stimulative action of light in chemical processes is well illustrated in the matter of formation and maintenance of chlorophyl. Protoplasm is capable of constructing this complex and unstable substance in darkness, and of maintaining it in a fairly normal condition for periods extending over many months. In many species however, the process of formation is not set up except under the stimulation of light, and the entire spectrum appears to participate in the stimulation. Simultaneously, however, the upper end of the spectrum exerts a disintegrating action, which is probably a direct chemical effect of the same character as that by which enzymes are broken down.

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[141] MacDougal. Practical Text-book of Plant Physiology, 110. 1901.

Radiant energy in the form of light being the most important source of energy of plants, it enters into manifold physiological relations with the shoot. The plant has coördinately a number of capacities for adjustment to various phases, degree of intensity, and angle of incidence of the rays. An added interest is attached to this feature of the subject from the fact that the capacity for these adaptive reactions have been formed to respond to associated characters rather than to the exact portion of the spectrum with which the action of the plant is concerned. Thus the phototropic reactions of plants are induced in greater part by the more refrangible blue violet rays, the resulting movements being for the direct purpose of placing the surfaces of the chlorophyl-bearing organs at a proper angle for the economical and safe reception of the orange red rays. It is true of course that the two kinds of radiations are almost invariably associated so far as the experience of the vegetable world is concerned, but the fact remains that the stimulation in question is one of association. A further example of such associations in irritability is to be found in the sensibility of reproductive organs to light. Seeds and spores are benefited directly in a few instances only, by exposure to light, yet the conditions for the distribution of seeds and spores are more commonly favorable when the reproductive organs are held up in sunlight. Here the phototropic response is made to a stimulus ordinarily associated with a series of complex conditions embracing currents of air, activities of animals useful in dissemination, water, etc., which are actually necessary for the profitable and successful dispersal of the propagating bodies. Even the germination of a large number of seeds and spores in light only may be regarded as a similar association of a stimulus with other vegetative conditions. It is true of course that spores of certain pteridophytes must have light-exposure to enable the chlorophyl-apparatus to construct building material for germination and growth, but in the larger number of instances illumination acts simply as a signal indicative of the presence of other necessary factors.

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[142] MacDougal. Critical points in the relations of light to plants. A résumé read before the Society of Plant Physiology and Morphology, Baltimore, Dec. 28, 1900. Abstract in Science, 13: 252. 1901.

The intensity of light necessary to constitute a phototropic stimulus varies enormously with different species, and with the developmental state of the individual. Using a normal candle burning 7.78 grams of paraffine per hour at a distance of one meter as a standard it has been found that an illumination of .00033 to .06 meter candle constitutes the minimum in seedlings of the most delicately organized species examined. The optimum effect in curvature is obtained in the same plants with an intensity of .11 to .44 meter candle, and these intensities must be increased a hundred to a thousand times to reach the maximum. Increase of the intensity beyond the maximum may result in changing the character of the response in such manner that the organism will curve or move away from the source of the rays. The more refrangible rays are chiefly active in such effects, and the amount of increase in the intensity necessary to constitute a stimulus is not more than 18 per cent. in some instances.

In addition to the reactions described above the plant shows other forms of response to intensities of illumination by photeolic and photolytic movements which bring the cell-constituents into adaptive relations with radiant energy by which injurious activity of the transpiratory and other functions are avoided. All efforts to establish a connection between the action of light on the enzymes or other cell contents as a primal and direct cause of the reactions in question have failed.

Light has undoubtedly exerted a predominating influence in the development of the prevailing types of vegetation, the form and structure of the body and its members being largely determined by the experience of the plant with respect to the nature, intensity, and direction of the rays which have impinged upon them. It would hardly be justifiable to say that light has originated or caused dorsiventrality in the vegetable kingdom: the causes must lie deeper and be infinitely more complex. Light of course has been one of the complex conditions to which dorsiventrality is a primary and basic developmental adaptation. Given the capacity of dorsiventral organization or development however in individuals, and its occurrence is often directly subject to the determinative and inductive action of illumination. It is to be said in this connection that the use of the term "directive" to designate morphogenic influences exerted by light, as has been done by Goebel, is withal, not in harmony with current usage, this term having long been applied to the action of the rays in inducing phototropic, photeolic and photolytic movements of the axes of the shoot and its members or of the body in general.[143]

Chief among the determinative influences exerted by light are to be mentioned the anatomical differentiations which may ensue as a result of its action, by which an organ may become dorsiventral and the positions of the dorsal and ventral surfaces altered. It is well known however that any form of dorsiventrality once assumed by the body or any of its members may not be changed, or reduced by altered conditions of illumination. A second phase of induced bilaterality is that in which organs are induced or suppressed upon complementary surfaces. This form of symmetry is often directly reversible by changed conditions of illumination, particularly among the thallus-like forms of the lower plants. Not only does the illumination determine the relative position of the dorsal and ventral surfaces, but it may also guide the polar differentiation, the apex and base of plant-axes being formed in developing spores with respect to the direction of the rays.

The association of different developmental stages of a plant with various intensities of illumination and the hindrance of procedure in every other instance in which the intensity of the light is beyond certain limits is a somewhat more complicated and delicate manifestation of the determinative influence of light upon the induction or suppression of organs. The action in question must be purely stimulative in its character, and for every stage an optimum, maximum and minimum of intensity might theoretically be established.

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[143] Goebel. Influence of Light. Organography of Plants. Eng. Ed., 227–259. 1900.

The length of the main axis and its branches, and the superficial extent of foliar organs have been found to depend upon the intensity of the illumination in a large number of species. Such variations in stature are coupled with corresponding alterations in internal structure. Adaptations of this character may be generally attributed to responses to the transpiratory conditions set up and to various mechanical factors. The marked features of alpine types consisting chiefly of dwarfing of the shoot and additional checks upon transpiration may be ascribed in part to the increased intensity of the illumination at higher levels due chiefly to the lessened absorption by the atmosphere of the blue-violet end of the spectrum, and to the altered moisture-relations by which the danger of drying out is much greater than upon plants at lower levels.

The change of the light-conditions entailed when aërial members are converted functionally into underground organs is over-balanced by the altered mechanical conditions, so that only a part of the differences may be ascribed to altered illumination. The character of the stresses to be borne are so altered that the development and arrangement of the mechanical tissues are necessarily different from those of homologous aërial stems. Then again, the humidity of the medium is so much greater, and the transpiratory conditions so different that the epidermal surfaces and subepidermal tissues are widely variant from those of aërial stems and branches.

The terms "light" and "illumination" have been used in the preceding discussions to allude to the ordinary exposures of plants to daylight of an intensity varying with the local environment and longitude, and alternating with the nocturnal periods of darkness. A review of the records of investigations cited in the opening section of this book brings out most conclusively that the greater major-

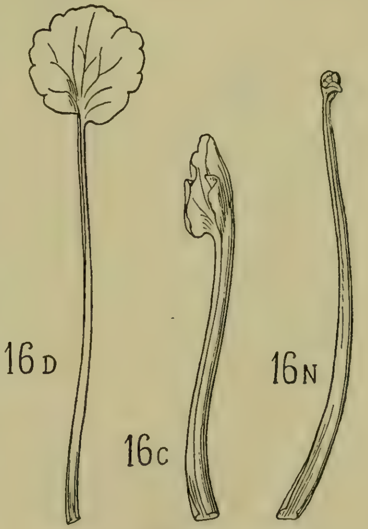

FIG. 157. *Ranunculus Asiaticus.* 16D, leaf developed in discontinuous normal illumination; 16C, leaf developed in continuous electrical illumination. 16N, etiolated leaf. After Bonnier.

ity of plants exhibit divergences from normal growth and development whenever cultivated under conditions in which the customary occurrence of illumination and darkness is varied. The effect of one departure, in which plants are cultivated in complete darkness, has been the subject of an enormous number of investigations as previously indicated. The amount of experimental evidence at hand bearing upon the influence of continuous illumination upon plants is comparatively meager, the most important contribution to the subject, from a botanical point of view, having been made by Bonnier in 1895 (see page 27 of this Memoir).[144]

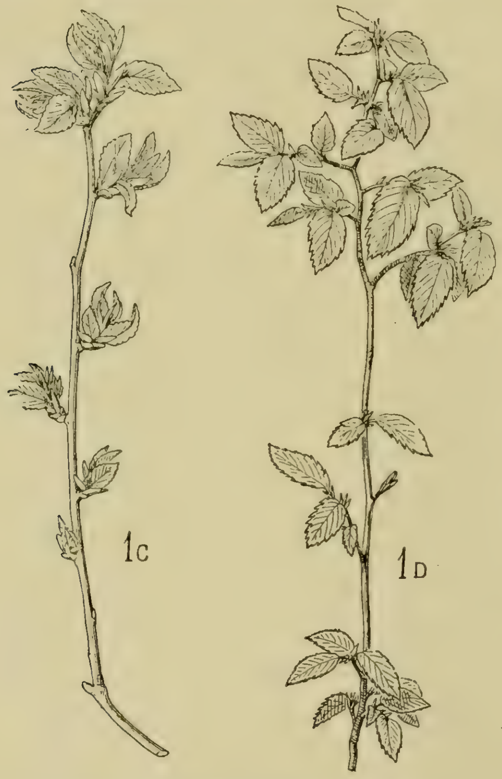

FIG. 158. *Carpinus Betulus.* 1C, leafy branch from small tree in continuous electrical illumination. 1D, leafy branch in normal discontinuous illumination. After Bonnier.

The continuous electric illumination to which Bonnier subjected the plants used in his experiments was of such intensity that a liberation of oxygen from aquatic plants under the same conditions took place at about one third the normal rate at which the process ensued in sunlight. Particular emphasis is to be laid upon this fact in view of the well-grounded conclusions, to which reference is made above (p. 204), that the separate stages of development of a plant, or of the different organs, are associated with certain intensities of illumination. An intensity below the normal of full sunshine would be favorable for certain action and unfavorable for others, and it is to this continuous and long-continued condition uniformly favorable to the growth of certain organs and tissues, that the aspect of plants grown in uninterrupted illumination must be ascribed rather than to any green "etiolative" effect supposed to be produced. Thus in continuous exposure to illumination by Bonnier, a much greater development of chloroplasts and formation of chlorophyl ensued than in the normal; the bark, and practically all of the parenchymatous tissues containing chlorophyl even to the central pith. The tissues of the leaf did not reach the extreme stages of differentiation characteristic of normally exposed organs and the same may be said of the stem in which the parenchymatous tissues showed but little differentiation; bark was not developed, and endoderm was not always distinguishable. In the case of the hellebore special alterations in the development of the endoderm and pericycle were noted. Because of the general arrest of the morphological development of the stem, which in the very nature of the plant must be similar in some respects to those resulting from etiolation, or any other cause retarding development, it may not be concluded that the two processes are similar. So far as the results of Bonnier may be interpreted, the exposure to the illumination in question showed no especial feature due to the continuity of the illumination, but may rather be ascribed to the accentuated effects of an illumination of low intensity.

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[144] Bonnier, G. Influence de la lumière électrique continue sur la forme et la structure des plantes. Rev. Gen. d. Bot. 7: 241, 269, 332, 407. 1895.

Schübeler[145] transported a number of cultivated and native species from lower latitudes to places in the northern part of Scandinavian peninsula where they would be subjected to a continuous illumination during a period of two months, during which the sun remains above the horizon in that locality. It is to be noted that the intensity of such illumination is far below that of temperate and tropical localities. The vegetative period of such species was notably shortened, and the seeds produced were larger than the average. The effect of such continuous illumination was to cause an accumulation or increase in the amount of certain aromatic and flavoring substances, and to increase the amount of coloring matter in leaves and flowers, while diminishing the amount of saccharine matter present. A specimen of *Acacia lophantha* did not show any of the usual diurnal adaptive movements of the leaflets according to this account during the two-months-long day.[146]

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[145] Schübeler. The effects of uninterrupted sunlight on plants. Abstract in Nature, 21: 311. 1880.

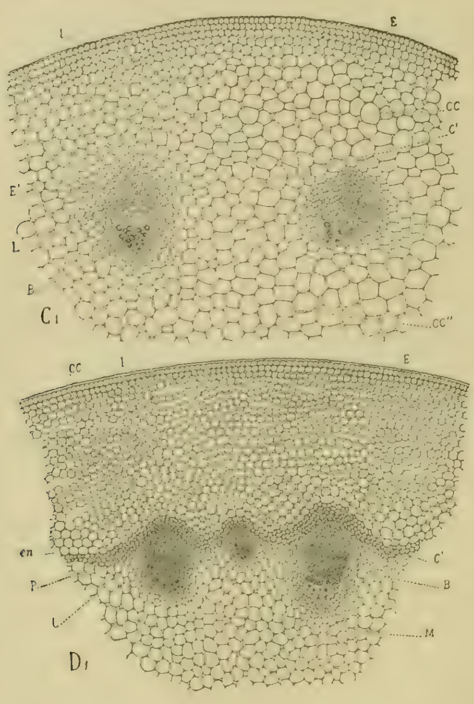

FIG. 159. *Helleborus niger.* D, section of basal portion of petiole of normal leaf. C, section of basal portion of petiole grown in continuous electrical illumination. E, epidermis. CC, cortical tissue. L, bast fibers. B, wood cells. *en*, endodermis of entire stele. E′, endodermis of separate bundles in etiolated petioles. C′, pericyle. CC″, parenchymatous cells in position of medulla. After Bonnier.

The influence of illuminations of a duration and intensity different from the normal in the culture of economic plants has received some attention from physicists and horticulturists. Siemens[147] published a report of some experimental observations in 1880, in which the comparative behavior of plants in continuous darkness, normal daylight, normal daylight supplemented by nocturnal illumination from electric arcs, and electrical illumination for six hours daily, with confinement during the remainder of the day in a dark room, were described. The light from the lamps was of 1,400 candle power, measured photometrically, and was of such intensity as to injure leaves placed within three or four feet, an effect probably due in part to the high temperatures set up. Experiments in which the normal daily illumination was supplemented by nocturnal electrical illumination, showed the most vigorous growth and greatest development, and the same effect extended to the flowers and fruit. Nothing in the results described could be found to support the theory that light exerts a paratonic effect upon growth.

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[146] Wiesner, J. Untersuchungen ueber den Lichtgenuss der Pflanzen im Arktischen Gebiete. A. d. Sitzungsber. d. kaiserl. Akad. d. Wiss. i. Wien, **109**: Abth. 1, May, 1900.

[147] Siemens, C. W. On the influence of electric light upon vegetation and on certain physical principles involved. Nature, **21**: 456. 1880. See also Proc. Roy. Soc. 30: 210–230.

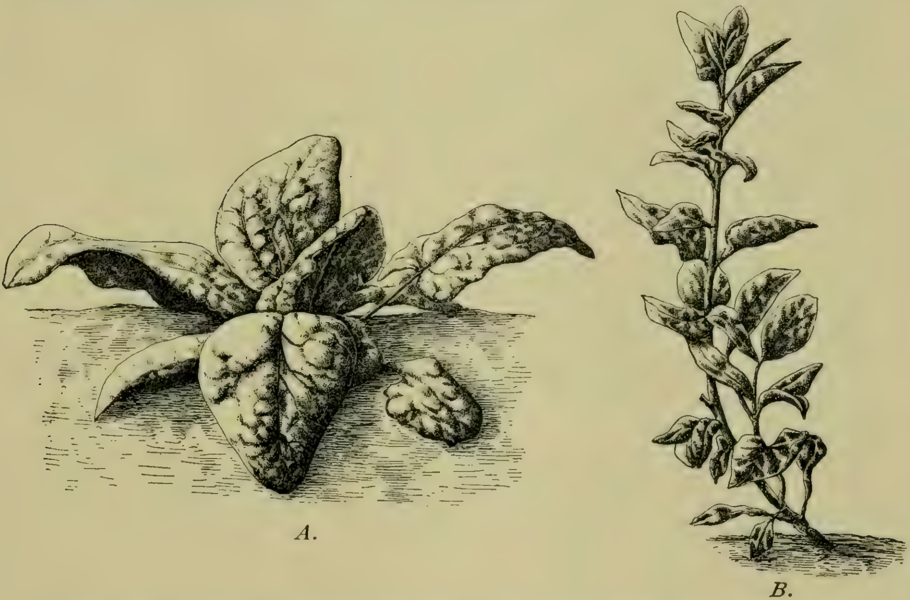

FIG. 160. Spinach (*Spinacia oleracea*). *A*, normal plant. *B*, specimen grown in daylight supplemented by nocturnal electrical illumination. Redrawn, after Bailey.

Deherain exposed a number of plants to continuous illumination from electric arcs in 1886. One series was cultivated in a darkened chamber, and another in a clear glass house. The lamps used were of a nominal candle power of 1,400 to 4,000 and the illumination (with the accompanying temperatures) was sufficient to produce many injurious effects upon the plants used. When the lamps were shaded by glass globes, less injurious effect was seen and some etiolative attenuations of stems and petioles were observed.[148]

[148] Ann. Agronom. 7: 551. 1881.

L. H. Bailey has carried out extensive experiments upon the influence of electric illumination of 2,000 candle power upon cultivated vegetables and flowers in which the normal daylight illumination was supplemented by that derived from electric arcs during nocturnal periods of various lengths. The rays from a naked arc were injurious to many forms and in the case of spinach it seemed to induce the formation of flowers and seeds after the manner of certain other agencies. The action of the light from shaded lamps was generally favorable to the growth of lettuce, while the effects on other plants were of advantage economically, or not,according to the portion of the body to be developed, and the general habit of growth. One of the most important results of the experiments by Professor Bailey [149] was that of attenuations similar to the "etiolations" of Bonnier were produced (see Fig. 160). The rate of growth observed in the continuous illuminations afforded no proof that light retards growth.

A comparative study of the injured and uninjured plants by Rowlee showed that such leaves as those of coleus and heliotrope were injured by the light from an arc lamp a yard distant, the effect of the light being to kill the epidermal cells and hairs. Thick, coriaceous, or succulent leaves with heavy cutinized external walls, such as those of *Ficus elastica*, *Rhododendron maximum*, *Kalmia latifolia*, and coronilla were uninjured by such exposures, doubtless owing to the screening effects of the heavy walls or cells containing much water.[150]

A series of experiments by Rane published in 1894 demonstrated that the light furnished by incandescent lamps 60 to 80 candle power did not give some of the injurious effects of arc lamps, and that the growth of foliage plants for food was accelerated by such illumination. Flowering plants blossomed earlier and continued to form flowers over a longer period than under normal illumination. Spinach and endive went quickly into the formation of seed under the same condition. This series of experiments was also lacking in results which gave any evidence that light directly retards growth.[151]

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[149] Bailey, L. H. Some preliminary studies of the influence of the electric arc lamp upon greenhouse plants. Bull. No. 30, Cornell Univ. Agric. Exp. Station. 1891.

Bailey, L. H. Second report upon electro-horticulture. Bull. No. 42, Cornell Univ. Agric. Exp. Station. 1892.

Bailey, L. H. Third report upon electro-horticulture. Bull. No. 55, Cornell Univ. Agric. Exp Station. 1893.

[150] Rowlee, W. W. Effect of the electric light upon the tissue of leaves. Proc. 19th Annual Meet. of the Soc. for Promotion of Agric. Science, Boston, Mass., pp. 50–58, 2 pls. 1898.

Corbett has recently published a paper upon the effects of an illumination derived from incandescent gas-light upon plants. The lamps furnished an illumination of about 560 candle power and a study was made of the influence at various distances. It was concluded that the effect of such light in supplementing the normal daylight produced heavier and taller specimens of lettuce, and induced faster growth of lettuce and spinach. Tomatoes produced flowers and fruits earlier than under normal illumination, and lettuce and radishes developed seed stalks earlier than under normal conditions. The rate and period of growth were increased in lettuce and spinach by the use of the supplementary artificial illumination. Lastly, the proportion of sugar in solution in beets grown in such extended illumination was greater than in the normal, although the size of the beets was less. As a general result the growth of the shoot, or the portion of it exposed to the light was greatly accelerated by the additional illumination afforded by the experiments.[152]

The entire life of the plant so far as the aërial organs is concerned is one of wide experience in alternating periods of daylight and darkness. The results of the experiments cited above demonstrate with some certainty that increases in the total duration of illumination to which a plant is exposed, during its vegetative period, either by artificial nocturnal illumination, or by cultivation in Arctic regions results simply in a correspondent acceleration of the seasonal development of the plant, by which a greater amount of work is accomplished within a given number of days. The extinction of the daily "resting period" brings no distinct reaction so far as important anatomical features are concerned, although an exaggerated production of certain substances is found to take place. Neither is any retarding or paratonic effect to be seen as a result of this continuous illumination.

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[151] Rane, F. Wm. Electro-horticulture with the incandescent lamp. Bull. No. 37, W. Virginia Exp. Station. 1894.

[152] Corbett, L. C. A study of the effect of incandescent gas-light upon growth. Bull. No. 62, W. Virginia Exp. Station. 1899.

See also Flammarion, C. Physical and meteorological researches, principally upon solar rays, made at the station of agricultural climatology, Juvisy, France. Abstr. Exper. Sta. Record, 10: 103. 1898.

A modification of the normal conditions by which the customary nocturnal period of darkness is lengthened to extend completely over the vegetative period, and to include the entire possible development of the plant exercises much more marked and quite sweeping effects. In the first place all of the direct influence of light is lacking, and in the analysis of the results of such etiolations it is necessary to take into account most rigidly the general relations of every species to light, as well its mode of life, seasonal habit, and mode of nutrition with respect to the accumulation and use of reserve food material.

The growth of a plant in darkness deprives it of the determinative and morphogenic influence of light in all of the various phases, and causes it to assume a stature wholly determined by its autotropic and geotropic reflexes and their correlations entirely uninfluenced by phototropic, or photolytic reactions. It is equally undeniable that etiolation must create most serious disturbances in the nutritive system. The photosynthetic power usually exhibited by chlorophyllaceous organs is wholly lacking, and if the plant is autotropic in its method of subsistence it must prosecute its entire development by the aid of reserve food laid up in its storage tissues. The amount of this material, even in seedlings, is usually far in excess of that needed for the stage of development for which it is provided, but when the plant is forced to depend upon this supply by confinement in the dark room, for the construction of organs and tissues usually supplied from the foliar organs, variations may be expected. These variations may consist in partial atrophy, or non-development of the organs concerned, and of alterations in the differentiation of the tracts conducting plastic material to and from the affected organs. The etiolative condition implies the establishment and maintenance of currents of plastic material by no means identical in volume, character, direction and location with those of the normal plant. Lastly, the relations of the body to water are most profoundly modified. The decrease in the formation of stomata, or the total failure of differentiation of these organs lessens the power of transpiration of the plant, and is followed of course by a much diminished movement of water and fluids in the body which must materially affect all translocation processes.

In addition to these negative effects of continued confinement in darkness the probability is near that darkness exerts a direct effect *per se* upon the plant, an aspect of the subject which will receive some consideration in the following pages.

It will be necessary to make a critical examination of the results of the observations described in the present memoir in order to determine how far the separate factors enumerated above are to be considered as responsible for the forms and activities of etiolated plants, and in order to test the validity of the various theories that have been proposed in explanation of the relations of plants to light and darkness.

The manifestations to be considered include among other features alterations in the seasonal or periodic activity coupled with alterations in the duration or length of existence of the various members of the shoot. These departures from the normal mode of existence serve as a means of analysis of the economic value of the reserve supplies in seeds and other storage organs. It follows naturally that the form and general aspect of the shoot are greatly altered by a development in which the usual relation to light is disturbed, and that such divergences are accompanied by unusual methods of differentiation of tissues, which are developed in a manner markedly different from the normal, some being suppressed, others accentuated, and in some instances new tissues arising. Variations occur in the form, size, and number of the elements, the structure and character of the walls being materially different from the normal, while the protoplasts diverge chiefly in the character of the inclusions, and composition of the vacuolar fluids. Organs and members may be suppressed, or undergo a development of mass beyond the normal in a manner wholly determined by the general physiological relations of the species in question. The abnomalities may go even deeper and include variations in the dorsiventral organization of the plant, necessarily accompanied by alterations in the character of the reflexes exhibited; many of the more important forms of irritability being suppressed. The non-development of the various stimulative reactions is purely a loss of functional capacity in some instances, while in others the change from the normal is still more sweeping and embraces the non-formation of the tissues in which the power of reaction is ordinarily invested. The relations of light and darkness to reproductive organs and their products are so complex that an interpretation of the behavior of these mechanisms may be made only after a consideration of the mode of formation of the reproductive bodies, and of the method of their dissemination, as well as of the general features of the nutrition of the plantlet arising or developing from such bodies.

A general examination of the results at hand may be made by a recapitulation of the principal facts disclosed as to the etiolative and other reactions exhibited by the different members and organs of the bodies of the simpler and higher plants.

Stems and main axes in general exhibit the greatest diversity of behavior in the matter of growth in length and thickness, final extension and duration under etiolative conditions. The least deviations from the normal occurs in species in which the main axis is subterranean or is ordinarily shielded from the direct action of light. Such plants usually send up leaves and flowers during the vegetative season with die back periodically, to the underground or shaded portion. The aërial organs thus produced, leaves, inflorescences and branches, undergo etiolations that will be described below, and their altered development is not without correlation effects upon the axis of the plant not directly exposed to the action of the rays.

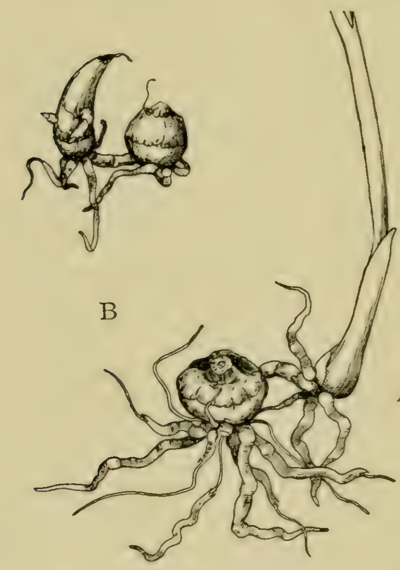

FIG. 161. *Aplectrum spicatum*. A, spent corm with young corm bearing a leaf. *B*, resting corms, one of which was formed under normal conditions, and the other is attenuated from being formed in darkness.

Effect of Etiolation on Bulbs, Tubers, Corms and Rhizomes. — In species in which the stem is compressed and clothed with scale-leaves in the form of a bulb as in *Allium* (pp. 37, 39), *Amaryllis* (p. 40), *Bowiea* (p. 82), *Hemerocallis* (p. 113), *Hyacinthus* (p. 117), *Narcissus* (p. 128), *Ornithogallum* (p. 120), *Quamassia* (p. 87), *Sparaxis* (p. 180), *Tritelia* (p. 182), *Tulipa* (p. 185) and others of the same type but little alteration ensues, except that the bulbs or stems developed as storage and propagative organs at the end of the season in the dark room are necessarily smaller than the parent bulb of the last growth in the open, by reason of the diminished amount of material available for construction and the diminished surplus for which storage is to be provided. The same is also generally true of solid tubers and corms like *Aristolochia* (p. 71), *Arisaema* (pp. 48, 50), *Calla* (p. 87), *Caladium* (p. 85), *Peltandra* (p. 144) and others of this type, the newly-formed part of such structures being more slender when formed at the bases of etiolated branches, inflorescences and leaves. In the last-named instances, however, in addition to having a lessened need of storage tissue the etiolation of the aërial organ undoubtedly exerts an additional stimulation by which more attenuated forms result. This action is the converse of that seen in partial etiolations in which illuminated organs exert a stimulative effect on others in darkness. The former phase of the reaction is most highly accentuated in *Aplectrum* (p. 46) and *Tipularia* (p. 181) of the plants studied. In these two species the vegetative season is characterized by the formation of one or more offsets from the corms, the terminal internodes of which become apogeotropic, assume an upright position and become thickened into a corm, bearing a single leaf from the uppermost internodes. The leaves are much longer than the normal and do not completely expand, remaining in a plicately folded position in the darkness. This attenuation is also participated in by the internodes from which the corm is formed, a length nearly double that of the normal being reached, with a diameter less than the normal (Fig. 161).

The creeping rhizome of *Sansevieria* offers an example of a diageotropic stem which undergoes alterations in its geotropic properties during etiolation, becoming apogeotropic and assuming an upright attitude, the structure becoming entirely radial (p. 171).[153]

A similar action is exhibited by *Nuphar luteum* according to Goebel, the creeping rhizome assuming an erect position, and undergoing alteration from a dorsiventral to a radial structure when covered with earth; the effect in question is ascribed to darkness, and is said to be exhibited by many spermatophyta.[154]

Effects of Etiolation on Aquatics.—The photomorphotic relations of rooted and submerged aquatic plants are by no means simple, and reactions are so highly diverse that a general treatment is all but impossible. The stems or modified branches bearing floating organs of *Nuphar*, *Nymphaea*, and other species which anchor to the substratum have been shown by Frank to have a capacity for adaptation to the depth of the water, which seems to be independent of effects of alterations in intensity of illumination. A similar reaction is seen in *Hydrocharis morsus-ranae* when the stature of the petioles of swimming and stranded plants is compared. The elongation of stems submerged below the normal depth is accomplished by an excessive growth of the usual number of internodes rather than by any multiplication of these members in all of the observations which have been brought to the author's attention.[155]

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[153] Maige, A. Recherches biologiques sur les plantes rampantes. Ann. Sc. Nat. Bot. Ser. 8, **11**: 345. 1900.

[154] Goebel, G. Organography of Plants. Part 1, p. 231. 1900.

Noll has recently proposed that all such such adaptations by which the the length and character of supporting organs are altered in order to bring about a better adjustment with the medium or substratum should be included under the general head of etiolations, which might be distinguished according to the nature of the cause. Thus the well-known reactions of plants to darkness would be designated as *darkness-etiolations*, while the modifications due to the depth of the water would be *water-etiolations*. The same author has also proposed that the specific morphogenic influence of darkness upon plants should be known as *skototonus* in antithesis to *phototonus*. The former term is acceptable as it suggests a definite term for a phase of reaction on the plant of the plant, which, as previously pointed out by the author, and emphasized by Noll, is not due simply to the absence of the effects of light, but is the reaction to a definite condition.[156]

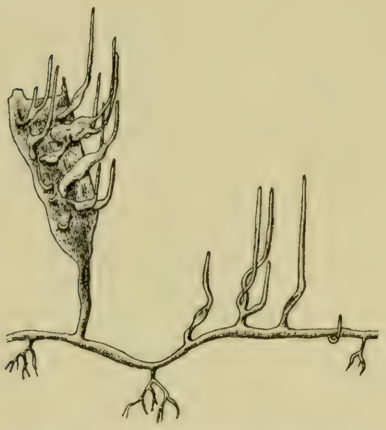

FIG. 162. *Caulerpa* with cylindrical branches formed in darkness. Redrawn, after Klemm.

Rooted aquatics such as *Calla palustris* (see page 87) and *Peltandra Virginica* (see page 144) were found to undergo a slightly excessive elongation of the petioles when confined in darkness, and *Saururus cernuus* (see page 179) developed stems in excess of the normal length under the same conditions. It is to be noted that these three species are, properly speaking, bog plants and support their inflorescences and foliar organs above the level of the water. A similar behavior has been reported for *Hippuris vulgaris*, *Ranunculus divaricatus* and *Myriophyllum spicatum* by Möbius, so that the evidence is fairly conclusive that aquatics or semi-aquatics, which carry up the shoots irrespective of the exact height of the water level agree with land forms in their etiolative reactions.[157]

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[155] Fank, A. B. Ueber die Lage und Richtung schwimmender und submerser Pflanzentheile. Cohn's Beitr. z. Biol. d. Pflanze, 1: Hft. 2. 31–86. 1872.

[156] Noll, F. Ueber das Etiolement. Separate a. d. Sitzungsber. d. Nied-Rhein. Gesell. f. Natur- u. Heilkunde z. Bonn. 1901.

MacDougal, D. T. Critical points in the relations of light to plants. Read before the Society for Plant Physiology and Morphology, Baltimore Meeting, Dec. 28, 1900. Abstract in Science, 13: 252. 1901.

The results attained by Möbius with other forms are fairly in accord with those of Frank so far as the action of stems is concerned. *Naias major*, *Cabomba*, *Chara* and *Callitriche* showed no special reactions to confinement in darkness. *Philotria Canadensis* (*Elodea Canadensis*) and *Ceratophyllum demersum* occupy a position midway between the two groups of forms noted above. Both species are rooted aquatics with the shoots wholly submerged, and yet show an exaggerated elongation of the internodes in darkness, even when torn from their anchorage and allowed to float freely in the water. The flowers of *Ceratophyllum* are borne in submerged axils, and those of *Philotria* float on the surface, the staminate ones becoming detached and rising to the surface when mature. These etiolative elongations are accompanied by various reflexive movements of the leaves in *Ceratophyllum* and *Myriophyllum*. No explanation is at hand to account for the characteristic behavior of the two forms noted above. It may only be said that these two plants are exceptions to the rule that submerged and floating aquatics are not capable of etiolation. It is to be noted in this connection that the submerged forms of at least some of the species with dimorphic leaves are due to the osmotic action of the salts dissolved in the water, or rather to the amount of water held in the vacuoles of the primordia. This has been shown to be the case in *Proserpinaca palustris* and is very probably true of other forms also.[158]

The elongated cylindrical prolifications formed by *Caulerpa* in darkness may be taken to be due in part to the specific influence of darkness, and in part to the absence of the formative influence of light, by which dorsiventrality is wholly lacking from etiolated organs. The reactions of *Caulerpa* in the dark chamber are to be classed with those exhibited by *Ceratophyllum* and *Philotria* as being entirely independent of pressure, since the reactions in question are exhibited by isolated floating fragments of shoots.[159]

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[157] Möbius, M. Ueber einige an Wasserpflanzen beobachtete Reizarscheinungen. Biol. Centralblatt, 15: 1, 33. 1895.

[158] MacCallum, W. B. On the nature of the stimulus causing the change of form and structure of *Proserpinaca palustris*. Bot. Gazette, 24: 93. 1902.

Duration of Etiolated Organs and Plants.— The actual duration of etiolated organs formed and confined in darkness varies greatly with the degree and mode of development of these organs, and is greatly influenced by the transpiratory relations of the shoot, a subject which will be discussed below. The length of time, or number of seasonal periods through which an ordinary chlorophyllose autotropic species may exist, when confined in a dark room, is determined by a number of factors. It is to be said that the data bearing upon this subject, as noted in my observations, are by no means to be taken as to express the ultimate endurance of the species tested since a modification of the temperature and moisture to meet the special needs of the separate species would doubtless result in extending the periods much beyond the limits given. If the plant produced in darkness simply the number of stems, branches or foliar organs usually developed in one season, the question became one of the endurance of the separate organs, and the greater majority of the species examined perished with the death and maturity of such etiolated members, many of them being incapable of further existence upon the reduced supply of available reserved food.

In one series of forms the failure of the earlier organs formed in darkness to reach illumination was followed by the extension of the shoot by excessive elongation of the internodes, and the multiplication of these members and the dependent branches, in a manner giving an epitome of the life of the normal plant. Thus, in the seedlings of *AEsculus*, *Hicoria* and others, the young plantlets developed many more internodes than the normal, the foliar organs of which quickly perished, the entire growth representing a series of efforts to spread chlorophyllose tissues in the light. This capacity in seedlings in the way of continuous effort, seems to reach its maximum in the cocoanut, which continued a growth of the plantlet for fifteen months without interruption, being nourished saprophytically upon the carbohydrates, fats and proteids, stored in the huge endosperm.

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[159] See references to Berthold, Noll and Klemm on page 25 of this memoir.

At the end of this period half of the material originally stored still remained in a normal condition, and it seems entirely probable that the seedling of this species might be capable of living two or three years in total darkness, receiving only water and mineral salts from the substratum. No evidence has been afforded by my experiments that any adaptation to continued darkness, was made by an increased capacity for taking up organic matter from the soil.

Continuous growth resulting in the formation of a number of leaves far in excess of that shown in an ordinary season, was observed in *Canna*, which developed etiolated leaves vigorously and continuously for four months. *Caladium* (p. 85), which continued sending up leaves for a period of twenty months in darkness before the underground member perished, and *Rumex* (p. 170), which sent up a succession of leaves for eight months are also examples of this type. The slow growth of succulents in darkness is of a similar character. *Opuntia* (p. 131), makes a steady extension of the curious cylindrical etiolated shoots through long periods of darkness. *Gasteria* (p. 110), was found to continue the extension of its aërial shoot for eighteen months in total darkness, and *Sansevieria* (p. 171) for a period of twenty months, by means of food stored up in the underground stems and succulent leaves.

The endurance of plants which undergo seasonal periods of inactivity in darkness gives the question a new aspect. In one series inclusive of *Apios* (p. 42), *Aristolochia* (p. 71), and *Cyclamen* (p. 100), shoots are sent up from the tuberous underground organs which undergo a characteristic etiolative development, and then perish, the plastic contents of the newly formed members being transported back into the storage organs. At the close of the season, the amount of material in such organs is less the amount used in respiration, and the portion that has been converted into aplastic substances in the aërial organs. The principal changes in the storage organs of plants of this type consist in slow increases in size during a number of seasons until destroyed by some contingency, or reach some limit of growth at present unknown. The external layers of such members are generally well protected by corky or other resistant layers, and do not decrease in size during the withdrawal of the material necessary in the construction of the aërial shoots.

A larger group of the species brought under observation have underground organs in the form of rhizomes and corms in which a new section is added to the apical portion during the seasonal activity, and the oldest portion is abandoned and cut off from the surviving region, examples being furnished by *Arisaema* (pp. 48, 50), *Trillium* (pp. 181, 182), *Arodes* (p. 86), *Amorphophallus* (p. 40), *Filix* (p. 106), *Menispermum* (p. 125), *Onoclea* (p. 129), *Osmunda* (p. 132), *Peltandra* (p. 144), *Podophyllum* (p. 150), *Polystichum* (p. 147), *Pteris* (p. 157), *Viola* (p. 186) and *Woodwardia* (p. 188). Plants of this type seemed to be admirably adapted for several seasons activity in uninterrupted darkness. The action of the apical bud generally resulted in the formation of a terminal region of smaller diameter than the normal, and as the rhizomes or corms were cut away in the older portions the underground member left at the end of the season of growth in darkness would be smaller than the normal average. The aerial organs sent up for such diminished underground members were also smaller than the normal, and showed a tendency to appear in lessened number. The most striking example of this nutritive type is that of *Arisaema* (pp. 48, 50), the corms of which were capable of four seasons of activity in the darkness under conditions of fairly constant temperature as described in an earlier section of this memoir. So far as the single set of analyses are to be considered as representative, the proportion of water increases in the aërial organs with successive etiolations, and decreases in the corms. The repeated development of the plant in the dark room without any accession of new material from the chlorophyl-apparatus seems to lead to the conclusion that the stored material contains the necessary constituents for cell construction, and the endurance of any species of the conditions under which no new food may be formed is primarily a matter of food supply. The capacity for such

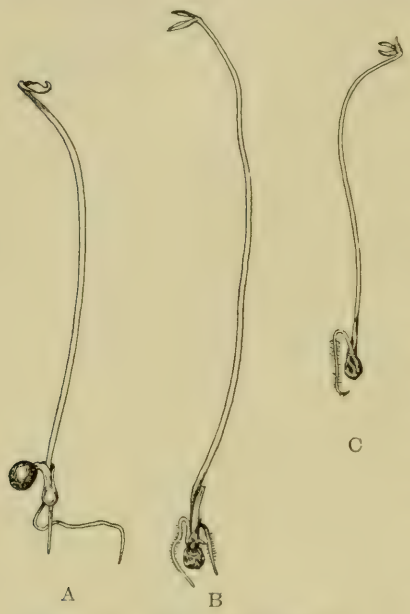

FIG. 161. *Arisaema triphyllum*. *A*, seedling after first growth in darkness. *B*, seedling after second etiolation. *C*, seedling after third etiolation.

repeated growth is a most effective device in the economy of species living in regions in which the upper layers of the substratum is loose and subject to shifting changes which might cover a plant too deeply for it to reach the surface during any given season. It is to be seen that *Arisaema* (pp. 48, 50) is capable of four distinct efforts to reach light and exposure to atmospheric factors. The seedlings of this plant exhibit this same adaptation in a remarkable degree, since the plantlet is capable of three seasonal efforts to bring its developing leaves up into sunlight. As has been described previously, *Arisaema Dracontium* (p. 48) and *Arum maculatum* naturally carry on the first season's growth of the plantlet without the development of chlorophyl-bearing organs, thus greatly lengthening the period of saprophytic nutrition of the seedling.[160]

A fourth type of endurance to prolonged periods of darkness is offered by species in which the old storage organs are destroyed during the period of formation of aërial organs from their buds, and new subterranean organs are developed on branches of the original organ or from lateral buds from the stems arising from them. *Aplectrum* (p. 46), *Bicuculla* (p. 80), *Solanum* (p. 180) and *Tipularia* (p. 181) may be cited as examples. The total duration of no one of these species has been tested, but the potato has been seen to form the second generation of tubers in darkness, and doubtless this species is capable of extended existence without light under proper conditions of temperature and moisture. In addition to the simple behavior of the corm in *Arisaema* (pp. 48, 50) noted above, the lateral buds may develop young corms and use up the material from the parent corm, continuing the existence of the plant in this manner.

It is to be seen therefore that an exposure of the aërial members of a plant to light is not an indispensable tonic condition for the plant. The subterranean members may continue their normal activity for several seasons when deprived of illumination, and with but little alteration in their structure, and that due directly to the amount of reserve material returned from the perishing etiolated members. In a few examples creeping stems which are only partially submerged or imbedded in the soil undergo changes in habit and function when placed in darkness, but such reactions must be taken as direct reactions to darkness rather than to any communicated impulse. Transmission of the etiolative impulse is to be seen in aërial shoots however.

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[160] MacDougal. Seedling of *Arisaema*. Torreya, 1 : 2. 1901.

Rennert, R. J. Seeds and Seedlings of *Arisaema triphyllum* and *Arisaema Dracontium*. Bull. Torr. Club, 29 : 37–54. 1902.

Aërial stems and aërial branches of plants with submerged stems will be considered in a common group in the present discussion. It is found that the references to etiolated stems in the greater part of the literature include both forms, and that no sharp distinctions have been made as to the main axis and its branches in the treatment of the relation of light and darkness to plants. The amount of branching and prolification of stem structures of all kinds in darkness is a very important feature of the reactions however and will receive attention in the following section of this memoir.

Effect of Darkness on Climbing Plants.—The aërial stems of plants that climb by twining, and by tendrils, examined during the course of my work include *Apios* (p. 42), *Aristolochia* (p. 71), *Bowiea* (p. 82), *Falcata* (p. 104), *Ibervillea* (p. 197), *Menispermum* (p. 125), and *Smilax* (p. 199). Of these *Apios* and *Aristolochia* develop stems that reach a length not far from the average normal, although the maximum length of stems in the open exceeds that of the maximum in darkness. The average length of the internodes in both of the above instances was far greater in the etiolated (see pages 43 and 71 of this memoir) than in the normal. Sachs found that the normal internodes of *Dioscorea Batatas* were longer than the etiolated, that but little difference was shown by the internodes in the hop vine and that etiolated internodes of *Bryonia dioica* were slightly longer than the normal when compared with regard to homologous positions in the shoot. As a result of a consideration of the data obtained by his observations Sachs was led to believe that by reason of their position in the stem some internodes had become permanently etiolated or that certain internodes inherited the etiolated habit, and did not undergo further elongation when compelled to grow in darkness. Thus he says: "Während die in der vorigen Abtheilung betrachteten Internodien durch die Beleuchtung in ihren Verlängerung gehindert werden, im Finstern aber ihrem Ausdehnungsstreben Genüge leisten, giebt es dagegen andere Internodien, welche selbts unter der Wirkung des vollen Tageslichts das Maximum ihres Längenwachstums erreichen können und daher durch die Finsterniss keine weitere Steigerung erfahren. Solche Internodien kann man gewissermassen als natürlich etiolirte be-

trachten oder besser wäre es vielleicht, sie als solche zu bezeichnen, deren Längenwachstum durch das Licht nicht wesentlich beeinflusst wird."[161] He seems to have lost sight of the differences in behavior among the internodes and to have transferred his idea of "natural etiolation" to include the entire stems. The measurements of etiolated and normal internodes given by him show that certain internodes in the stem of any given species undergo excessive elongation in darkness and others do not. His observations in this matter are confirmed by many others including my own, and it seems quite evident that the occurrence and position of internodes undergoing etiolative elongation are characteristic of the species and may have some connection with its general habit, and that no stem is to be regarded as "normally" etiolated.

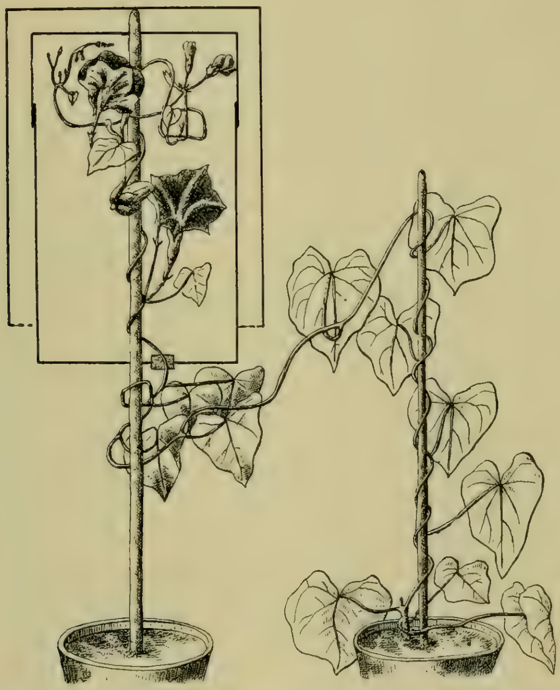

FIG. 164. *Ipomea purpurea*, with terminal portion of twining stem enclosed in a dark chamber illustrating the method by which "partial etiolations" are produced. Redrawn, after Sachs.

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[161] Sachs. Ueber den Einfluss des Tageslichts auf Neubildung und Entfaltung verschiedener Pflanzenorgane. Bot. Zeitung, 21: Beilage, p. 31. 1863.

Cotyledonary stalks of twining plants are excessively elongated in darkness in species in which the cotyledons are raised above the soil, but in others in which the cotyledons remain below the surface naturally, the first internode of the plumule takes up this action, and in some instances as in *Hicoria* (pp. 113–117), *AEsculus* (p. 191) and others in my own observations, the increase is shared by all of the succeeding internodes. This action is not confined to the climbing plants.

Alterations in the rate of growth and final length due to etiolation are variously distributed in climbing stems. The basal internodes of *Apios* show the greatest increase in length over the normal, while the median members are but little changed. The basal portion of the aërial stem of *Bowiea*, which is morphologically to be considered as an inflorescence axis is greatly elongated while the terminal braching portion is much dwarfed. The median internodes of *Bryonia* appear to exhibit a tendency to excessive elongation according to Sachs, the basal ones not reaching the normal size. The basal internodes of *Falcata* were elongated more excessively than the other portions of the stem, although all of the internodes were doubled in length. *Menispermum* did not develop internodes in any instance equal to the normal average, and the limited growth of this species in darkness, whether directly due to limited nutrition or not, yet is certainly conditioned by it, since the amount of reserve material in the slender rhizomes is very small. In *Phaseolus*, as tested in "partial" etiolations by Sachs the terminal internodes were much more elongated than the basal ones in darkness. It is to be seen, therefore, that the influence of darkness on climbing (twining) stems causes local disturbances of the rate of growth, and alterations in the location of the zone of maximum elongation.

Ibervillea is a tendril climber and the stems reached but a fraction of their normal length in darkness, the etiolated internodes being about normal length however. *Smilax*, which is also a tendril climber, sent up long shoots which were much less than the normal length. Extensive observations are not at hand, yet it is believed that multiplication of the internodes in darkness does not occur among twining plants, the reaction consisting wholly so far as length is concerned, in alterations in the length of internodes, which may not be equal to the normal in number.

Etiolated stems of climbing plants were prophototropic so far as my own observations go, and the capacity for the reaction to impinging rays of light seems to be inherited by individuals which have never been exposed to light except in the period of the integration of the seed from which they grew. The actual degree of sensi-

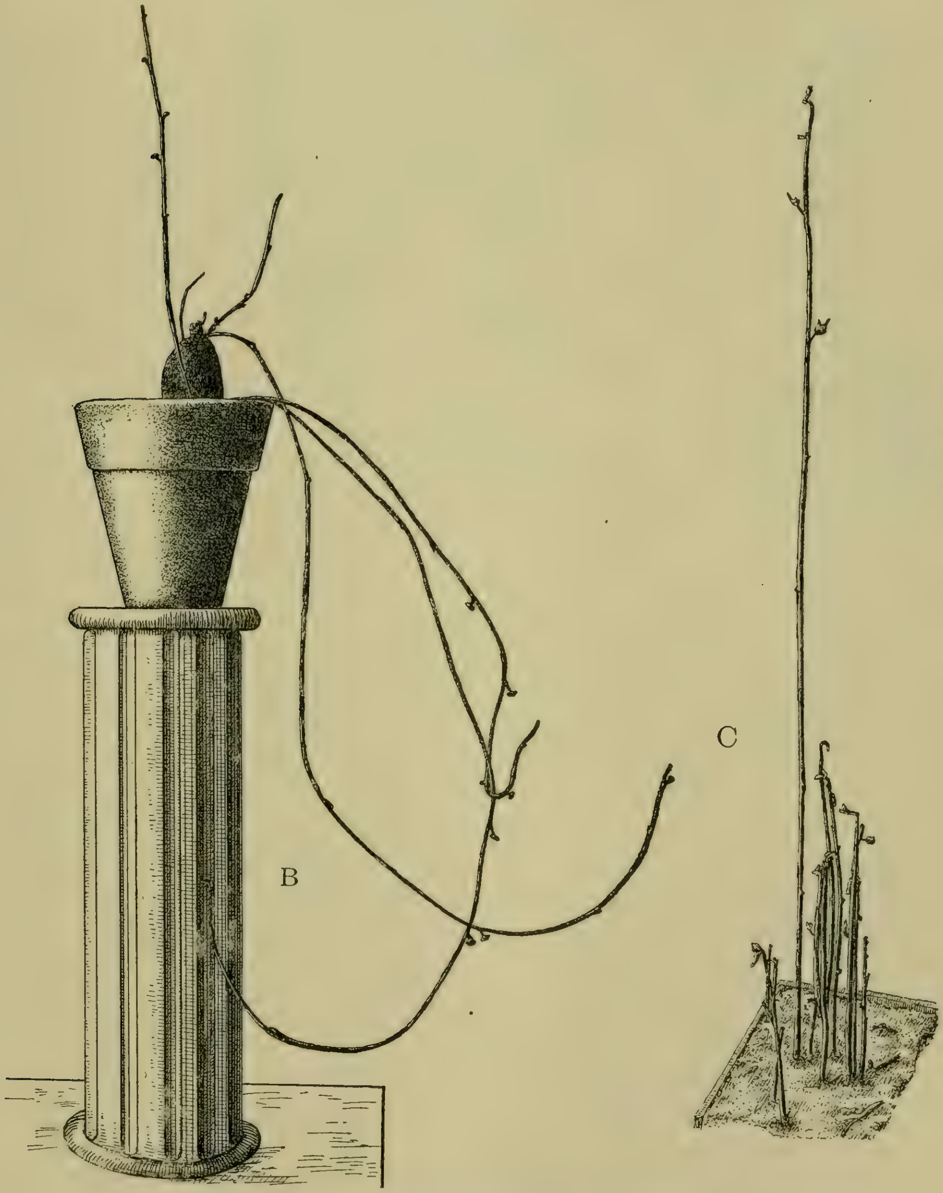

FIG. 165. *B*, etiolated stems of *Aristolochia*. *C*, etiolated stems of *Menispermum*.

tiveness is increased however, and etiolated plants show some divergence from the normal in reaction time and amount of increase in intensity necessary to constitute a stimulus.[162]

All of the climbing species examined in the dark room at the New York Botanical Garden were apogeotropic, and the stems assumed an erect position, falling over from their own weight as soon as a certain height had been reached. The development of *Menispermum* was accompanied by but slight manifestations of this character however, and the comparatively short stems remained in an upright position in most instances. It is most notable that none of the five species examined by the author, *Apios*, *Aristolochia*, *Bowiea*, *Falcata* and *Menispermum*, in which adequate stems were developed, were capable of twining around a support, although repeated tests of this particular phase of the reaction were made. Moreover the nutatory movements of the apices of the etiolated stems were of much narrower amplitude than in the normal.

Duchartre recorded that *Dioscorea Batatas* and *Manda suaveolens* did not exhibit twining in darkness when fully etiolated, but that when normal plants were brought into a dark room twining continued for some time, the apical portion of the stem finally assuming an upright attitude.[163] These results were confirmed by de Vries.[164] Sachs' experiments appear to offer evidence to the contrary, since he found that etiolated internodes of *Ipomaca purpurca* and *Phascolus multiflorus* were capable of attachment to a support by twining around it. An examination of his technique shows that such results were obtained in "partial" etiolations only, in which the apical portions of stems were thrust into small chambers through openings sealed with cotton, wool or other fiber, thus introducing the vitiating action of possible imperfect exclusion of darkness and the positive stimulative influence of light on the free portion of the stem.[165]

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[162] Figdor, W. Versuche ueber die heliotropische Empfindlichkeit der Pflanzen. Aus. d. Sitzungsber. d. kaiserl. Akad. d. Wiss. i. Wien, **102** : Abth. I. 1893. See references given in above paper to Wiesner's researches.

[163] Duchartre. Compt. Rend. **61** : 1142. 1865.

[164] De Vries. Zur Mechanik der Bewegungen von Schlingpflanzen. Arb. a. d. Bot. Inst. i. Wurzburg, **3** : 317. 1873.

[165] Sachs. Wirkung des Lichts auf die Blüthenbildung unter Vermittlung der Laubblätter. Bot. Zeitung, **23** : 117. 1865.

The results of observations upon etiolated seedlings appear to offer another phase of the question however. Both Sachs[166] and Noll[167] record that the stems of seedlings are capable of winding around supports even when fully etiolated. Noll grew seedlings of *Polygonum Fagopyrum*, *Tropaeolum majus* and *Brassica Napus* in a dark chamber under conditions that seemed to exclude all vitiation from the effects of light, obtaining marked circumnutations in half of the number of seedlings in some series of tests. The period of a single revolution of the growing tips ranged from eleven and a one-quarter hours to two hours. The stems of the seedlings of *Tropaeolum* and *Fagopyrum*, and in few instances those of *Brassica* also

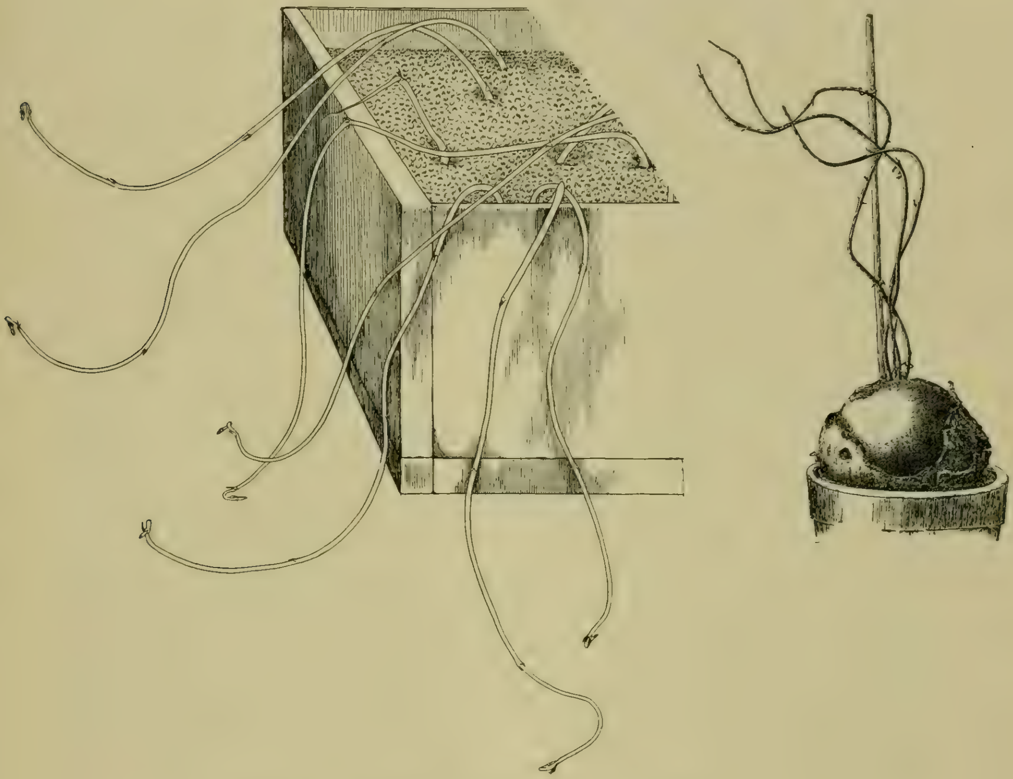

FIG. 166. Etiolated stems of *Apios*, and *Bowiea*.

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[166] Sachs. Vorlesungen ueber Pflanzenphysiologie. p. 668. 1882.

[167] Noll. Ueber rotirende Nutation an etiolirten Keimpflanzen. Bot. Zeitung, 43 : 664. 1885.

were found to be capable of twining around thin wooden rods supported in a vertical position. The action of the last-named species is held by Noll to indicate a method by which the twining habit might arise in any species with a pliant stem, in which torsions arise. In connection with the aspect of the subject under discussion in the present paper, this capacity for twining might be regarded as an inherited quality in the seedlings in question, and to be made possible by the torsions characteristic of certain etiolated stems of seedlings. So far as the evidence at hand is to be regarded as conclusive however, the power of twining is to be denied to fully etiolated adult stems; at least it may be said to be "not proven." It is by no means improbable however that it might be exhibited by seedlings and young stems arising from tubers or propagative bodies of some species.

The attenuated stems of climbers offer some evidence upon the effect of nutrition on development. The translocation of the necessary supply of constructive material from a basal reservoir through the long thin stems in which the cross section of the conducting tissues is very small, must result in a sufficiency of supply reaching the apical portion of the stem after a certain length has been reached. This upward transportation of carbohydrates is also rendered more difficult by the lack of development in the transpiratory organs. Scarcely any doubt remains that the insufficient food supply does operate to limit the stature of thin stems of all kinds, whether climbing or not.

The duration of the aërial etiolated shoots of climbers in some instances such as in *Apios*, *Aristolochia* and *Menispermum*, is fairly comparable to that of the normal. The delicate physical structure of etiolated stems makes the length of existence of organs grown in darkness more or less dependent upon the mechanical treatment which they receive from the experimenter. The lack of thickening in the epidermal walls, and of the mechanical and vascular tissues in general renders etiolated stems peculiarly liable to abrasions and wounds which quickly result in death. If care was taken that the action of air currents was excluded, and the etiolated organs were not handled or bent sharply the length of life was greatly extended, a fact also true of all etiolated organs, which in no instance were found to exhibit the power of forming calluses or closing wounds in an efficient manner unless brought into light. It is well known however that normally developed organs may form callus when confined in darkness.

The stems of etiolated climbers have been shown by various authors to be of normal thickness in some instances, greater than the normal in others, and less than the normal in others. Stems of *Apios*, *Aristolochia*, *Bowiea*, *Falcata*, *Menispermum*, *Ibervillea* and *Smilax* were thicker than the normal. The increase in diameter was due in all instances to an enlargement of the pith by increase in size of the elements, coupled with increase in the intercellular spaces in some cases, and also an increase in size and number of the elements of the cortical parenchyma with material alterations in the form of the cells in both instances. These plants share with all etiolated stems a lack of differentiation and development of the epidermal tissues. Trichomes were lacking in the etiolated stems of *Apios*, and were not so numerous on stems of *Menispermum* grown in darkness as on stems grown in light. The epidermal cells of *Apios* and *Falcata* were larger in all diameters than the normal, and smaller in *Menispermum*. Functional stomata were present in *Apios*, in increased number in *Aristolochia*, but were fairly normal in number in *Falcata* and *Menispermum*. Tissues of purely mechanical function in the subepidermal region and near the pericycle were lacking in development in all instances, while the stele here as in all etiolated stems remained in an embryonic condition. *Apios* presented a notable instance of the origin of a secondary generative layer in the pericyclic region similar to subterranean tuber-forming stems, although no other resemblance to these organs could be made out except, so far as the general increase of the parenchymatous tissues might be taken to be of this character.

Of the two species of tendril climbers examined, *Ibervillea* only bore these organs, and in a size but little less than the normal. The tendrils of *Smilax* are borne laterally on the hypopodial portions of the leaves, which appeared in darkness only as bract-like formations with the tendrils represented by minute papillae. The etiolated tendrils of *Ibervillea* were found to be irritable to contact, and encircled small rods of wood, but the free portion of the tendril between the engaged tip and the base was not thrown into spirals; a fact due among other causes to the lack of development of the mechanical tissues. Sachs found that the tendrils of *Cucurbita* not only clasped supports but the free portion passed into the spiral form in the "partial" etiolations made by him, and Von Mohl previously reported that the tendrils of etiolated plants of *Bryonia* were capable of a normal exercise of their functions in darkness.[168]

Growth and Development of Seedlings in Darkness. — Seedlings present more than one physiological type, and it will be profitable to divide them into several groups for the purposes of the present discussion. The species included in the present series of experiments include *AEsculus hippocastanum* (p. 191), *Arisaema Dracontium* (p. 48), *A. triphyllum* (p. 50), *Castanea dentata* (p. 91), *Cocos nucifera* (p. 95), *Coix Lachryma-Jobi* (p. 97), *Hicoria minima* (p. 114), *H. ovata* (p. 115), and *H.* sp. (p. 113), *Gleditsia triacanthos* (p. 113), *Phaseolus* sp. (p. 147), *Quercus palustris* (p. 158), *Q. rubra* (p. 159), and *Q.* sp. (p. 161), and *Ricinus communis* (p. 169).

Of the above species *Arisaema*, *Cocos*, *Coix*, *Ricinus*, as well as *Zea*, have a comparatively large quantity of reserve material stored in an endosperm, which in all instances except in *Ricinus* remains buried in the substratum until a certain amount of food material is withdrawn, and then the storage organ perishes. The degree of development and duration achieved by the seedling in such instances is dependent upon the amount of reserve food available in the seed, and the efficiency of its protection from decay and the attacks of fungi and bacteria. Thus in *Coix* the amount of material stored in the seed is not greater than in *Zea*, but the etiolated plantlets of the former attained a height much greater than the latter, in which but a fractional part of the starch and other material was absorbed by the seedling. Decay usually sets in early in the germination of the grain and the growth of etiolated seedlings of *Zea* soon ceases because of lack of food material. *Cocos* may be offered as an example of a device by which a comparatively enormous amount of food is stored up and protected from damage from external causes, nearly all of it being available to the developing plantlet. A seedling of this plant lived in the dark room for fifteen months saprophytically at the expense of the endosperm, and when examined at the close of this period had not used more than half of the total amount of the endosperm. During the interval, seven large leaves had been developed and an amount of growth carried on fully equal to the

[168] Sachs. Wirkung des Lichts auf die Blüthenbildung unter Vermittlung der Laubblätter. Bot. Zeitung, 23 : 119. 1865.

Von Mohl. Ueber den Bau und das Winden der Ranken und Schlingpflanzen. pp. 83, 84 and 122, 127. 1827.

normal performance of the plant. The above experience leads to the suggestion that the immense economic usefulness of *Zea* would justifiy a systematic attempt to develop races in which the endosperm would be more perfectly protected from the agencies which usually destroy it. The advantage gained from the use of the additional amount of food would accrue in a shortened vegetative period and stronger and healthier plants, resulting in a more abundant crop at the end of the season. It is more than probable, however, that the very processes of breeding of this species which have been carried on for the purpose of increasing the size of the grain, and the acquisition of the qualities that render it more suitable as an article of food have tended to weaken the protective devices of the grain, and to render it more liable to the attacks of destructive agencies.

The most remarkable species in the matter of the relation of the endosperm to the plantlet are to be found in the Araceae in which the seedling of *Arisaema Dracontium* and *Arum maculatum* may carry on their development during the first year after germination entirely at the expense of the material stored up in the seed even when under normal and suitable conditions. The other species, *Arisaema triphyllum*, with which the tests were made, showed the remarkable capacity of carrying on an amount of growth in darkness fully equal to the normal at the expense of the material stored in the seed. Beyond this it was capable of vegetative activity during the three succeeding seasons in the same manner, a manifestation not exhibited by any other plant, of which records are available. As a result of this action it is to be seen that the starch and other material in the endosperm is hydrolyzed by diastases secreted *in situ*, and in the embryo, and after being translocated to the body of the young plant is partially converted to the use of protoplasts, and into their enclosing membranes and included substances. With the death of the seedling nearly all of the plastic material, and the starch which has been laid down in the tissues of the plantlet are again translocated to the tuber formed at the base of the stem. Upon the beginning of a second season of growth the entire process is repeated except that in this, and in the succeeding seasons, the translocations simply move the material up and down the roots and stems of the young plants. The residuum of plastic material thus undergoes four major translocations and reconversions during the course of life of the seedling which lives three years in darkness.

In the single instance in which the endosperm is carried aloft, as illustrated in *Ricinus*, the amount of growth seems to be regulated directly by the amount of food present, which is nearly all available for the use of the developing plantlet. It is noticeable that this plant affords not only an exaggerated growth in length of the hypocotyl, but also allows the first internode of the plumule to reach a limited development. The stems of *Coix*, *Zea* and *Cocos* are slightly elongated in etiolated plants, while in *Arisaema* the stem takes the form of an underground tuber, the aërial portion consisting of the petiolated leaves, the tuber or corm being slightly attenuated as a result of the etiolation. In all of the above instances the excessive elongation consists chiefly in the increased length of a fairly normal number of internodes, although *Cocos* developed one more than the control specimens of the same age.

A second group of seedlings consisted of species of dicotyledonous woody plants with the reserve material present in large amount and contained in cotyledons which remained buried in the soil, including *AEsculus*, *Castanea*, *Hicoria* and *Quercus*. *AEsculus* usually develops one internode only during the first season of its growth, but the etiolated plants extended nine, the basal one of which was slightly longer than the normal. The various species of *Hicoria* and *Quercus* examined agreed in that the number of internodes was never greater than in the normal, except in one unknown *Quercus*, and in the case of *Q. palustris* was actually less. In all instances the etiolated stems were two or more times as long as the normal, the most excessive increase in length being witnessed in the basal internodes. The food material stored in the nuts of the seeds is quite perfectly protected from damage, and the greater part of it was available for the use of the plantlet. In consequence of this fact the duration and actual period over which growth extended was very long. In the case of a *Hicoria* the seedling went into a resting stage after a period of activity equal to a normal season and then resumed growth, making several branches. This repeated growth did not, however, entail the translocations and reconversions of energy characteristic of the seedlings of *Arisaema* as described above. The long-continued action of these woody seedlings implied some radical departures from the usual method of morphogenic procedure, which were most highly accentuated in the cortical tissues, and epidermal elements. The species in question form a distinct bark on normal plantlets, and all are characterized by exfoliating bark in the adult tree. The anatomical details of etiolated forms of this type will be described in a later section of this memoir. It may be said in this place however, that the transpiratory organs inclusive of lenticels were more sparsely developed than in the normal.

But two species of woody plants were examined in which the cotyledons served as the main storage organs, and were carried aloft during germination. *Gleditsia* developed the hypocotyl to a length 50 per cent. in excess of the normal, and the first internode of the plumule attained a length of 8 mm. The cotyledons were held in an appressed position, enduring through a period of sixty days, much longer than in the normal, and were thrown off only after their contents were completely exhausted. The other species, a *Phaseolus*, developed a hypocotyl longer than the normal; the contents of the cotyledons were entirely transferred, leaving but a small remnant which was cast off with the withered seed leaves. The amount of material thus laid down in the embryonic stem was sufficient to permit the growth of the first internode of the plumule to a length of three times the normal, and for the development of a pair of leaves with small laminae and attenuated petioles. The second internode was hindered in its growth by the exhaustion of the food supply. The difference in aspect of this plant and that of the terminal portion of partially etiolated adult stems was most noticeable.

The root systems of the various seedlings etiolated were incapable of exact comparison with those of control specimens, but in the main it appeared that the total length and general development of the roots of etiolated plants was not so great as in normal specimens. The growth of the root system would depend to a great extent, however, upon the transpiratory functions of the shoot, and as no etiolated shoot excretes more than a third or a half of the usual amount of water vapor, the effect of the lessened use of water would be reflected in a diminished development of the absorbent organs, which, in the greater majority of instances, also have less exacting demands upon them for mechanical rigidity as a means of anchorage.

It is difficult to estimate the value of the various records that have been made of this phase of etiolation, since the results in some instances were obtained by "partial etiolations," and in others the growth of the shoot may have begun before confinement in darkness, and then in still other instances the dark chambers were not absolutely exclusive of light. The examination of etiolating material in a dark chamber by opening a door that would admit daylight would of course vitiate the experiments by reason of the light stimulation ensuing in consequence of this exposure. Sachs says: "From the large seed of a bean or horse chestnut, on the contrary, there may be produced in the dark a plant of considerable size with copiously branched roots and several, though small and yellow, leaves."[169] The specimens of horse chestnut grown in my own experiments did not develop a root system in darkness equal to that in light. The sparseness of the root-system of this plant when etiolated is shown in Fig. 150. Detmer[170] noted the lack of full development of the roots of etiolated plants and ascribed it to the lack of the synthetic function of the leaves upon which the root-system was supposed to be directly dependent. But little doubt remains, however, that an etiolated shoot with lenticellar openings, stomata and other transpiratory devices, would necessarily be accompanied by a more fully developed absorbing system than one in which but little water was taken up or used by the shoot. Vogel relates that the roots of plants grown in darkness are more developed than those which have been cultivated in light, a statement put forward by him as a result of measurements of the aërial and submerged roots of *Bombax* and *Hura crepitans*, which does not afford any real proof of the statement in question, however. Lasareff found that the branches of adventitious roots of a large number of seedings were both fewer and shorter than in normal specimens, but he mistakenly supported the assertion credited to Famintzin by which such correlation was supposed to exist between the roots and shoots, that the longer the shoot of an etiolated plant, the shorter would be the root-system.[171]

Strehl[172] found that the rate of growth of roots of etiolated plants was generally greater than that of plants subject to the alternations of day and night for the brief period in which measurements were made, and this may be reasonably assigned to the undoubted correlation that exists between the rate of growth of the root and shoot, but so far as his data may be taken to bear upon this question in hand, the total amount of growth in etiolated roots was less than in the normal.

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[169] Sachs. Physiology of Plants. English Ed., p. 531. 1887.

[170] Detmer, W. Die Formbildung etiolirter Pflanzen. Vergleichende Physiologie des Keimungsprocesses der Samen. Pp. 464–478. 1880.

[171] Vogel, A. Beiträge zur Kenntniss des Verhältnisses zwischen Licht und Vegetation. Flora, **39**: 385. 1856.

Lasareff, N. Ueber die Wirkung des Etiolirens auf die Form der Stengel. Abstract by Batalin. Bot. Jahresber. **2**: 775. 1874.

[172] Strehl, R. Untersuchung ueber das Längenwachstum der Wurzel und des hypokotylen Glied. Leipzig, 1874.

C. Kraus[173] records his observations that the roots of etiolated plants do not reach the stature of normally cultivated plants, which he supposed was a direct correlation with the increased length of the shoot.

It appears as a consensus of the evidence upon this point that the root-systems of seedlings do not attain normal development when the shoot is fully etiolated. The numerous difficulties in the way of making accurate measurements have prevented the acquisition of data concerning the roots of adult perennial plants confined in the dark chamber during a vegetative season. The theories which attempt the explanation of this lessened development as a correlation with the increased length of the shoot have been found untenable from the fact that the length of the roots and shoot do not vary conversely as proven by Strehl. The supposition of Detmer that the lesser total length of the roots was due to the lack of material usually furnished by leaves is also quite beside the point, since this relatively diminished growth of the roots ensues when an ample supply of reserve material is present in the hypocotyls or endosperm from which it might readily be conveyed to the roots, and with much less expenditure of energy than from the leaves. The only causes which might affect the development of the root-system would be the use of water by the shoot and the demand for anchoring power or mechanical rigidity because of the strains exerted by the weight of a bending shoot. Etiolated shoots are erect, for the most part, and when disturbed easily and readily fall over, the roots being wholly inadequate to hold the shoots in position. It is well known, however, that the branching and growth of the root is quickly influenced by the conditions of absorption and transpiration affecting the shoot, and this feature is the only one which may be offered to account for the lessened development of the root-systems of etiolated plants, especially seedlings.

Effect of Darkness upon Succulents. — On account of the peculiar relations borne by the leaves of succulents to the stem it will be most profitable to consider the development of the entire shoot of succulents at the same time. The species which might be included under this head, that were used in my experiments comprise, *Agave Americana* (p. 37), *Gasteria disticha* (p. 109), *Opuntia Opuntia* (p. 131), and *Bowiea volubilis* (p. 82) might also be considered here, since its main axis consists of a succulent bulb imbedded in the upper layer of the substratum from which arises a slender inflorescence axis. The short thick stems of *Agave* which are completely sheathed by the bases of the fleshy leaves are not excessively elongated in darkness, the only reaction being shown by the leaves. Leaves partially developed when the specimens were placed in the dark room continued elongation, the newer basal portion being chlorophylless and yellow. The apical parts of such leaves maintained their original green color with but little change in the chlorophyl during periods as long as eight months. Leaves which were developed after etiolation of the plant had begun did not attain dimensions more than half of the normal, and were completely devoid of color, and showed a reduction of the marginal teeth and of other anatomical features. Stems of *Gasteria disticha* are usually very short, and are completely sheathed by the bases of the fleshy leaves, which are nearly double the length of the stem. During etiolation the stem elongates excessively by an increased growth of about the normal number of internodes, and the upper end of every internode becomes exposed and free from the sheathing leaf-base. The etiolated internodes were distinctly more slender than the normal. Still more attenuation was observed in lateral branches which are usually diagetropic and serve as propagating bodies. In etiolation these were erect and very slender, with internodes much elongated. *Opuntia* developed cylindrical stems with internodes slightly longer than in the normal flattened structures characteristic of this plant. The etiolated portions endured confinement to darkness for several months but were not so hardy as the normal stems, a fact probably due in part to the extremely delicate outer membrane which failed to protect the underlying tissues from mechanical damage in handling. The reduction of the transpiratory organs, and the comparatively moist air of the experimental chamber in which the plants were confined in darkness must also have contributed to the early demise of the etiolated specimens. *Bowiea* developed short thick inflorescence axes in darkness, with leaves slightly increased in size.

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[173] Kraus, C. Ueber einige Beziehungen des Lichtes zur Form- und Stoffbildung der Pflanzen. Flora, **61**: 145. 1878.

A notable feature of the behavior of succulents in darkness is their great endurance to exclusion from illumination, and also their capacity for the maintenance of chlorophyl for extended periods in the organs constructed in light. The reactions offered by *Gasteria*, of which the excessive lengthening of the stem is the most important are also to be seen in the Crassulaceae as examined by Brenner[174] and others. This author found that the growth of species of this family in moist chambers produced an excessive elongation of the stems, which continued only for a time, when the habit of developing short internodes and consequent rosettes of leaves was again resumed.

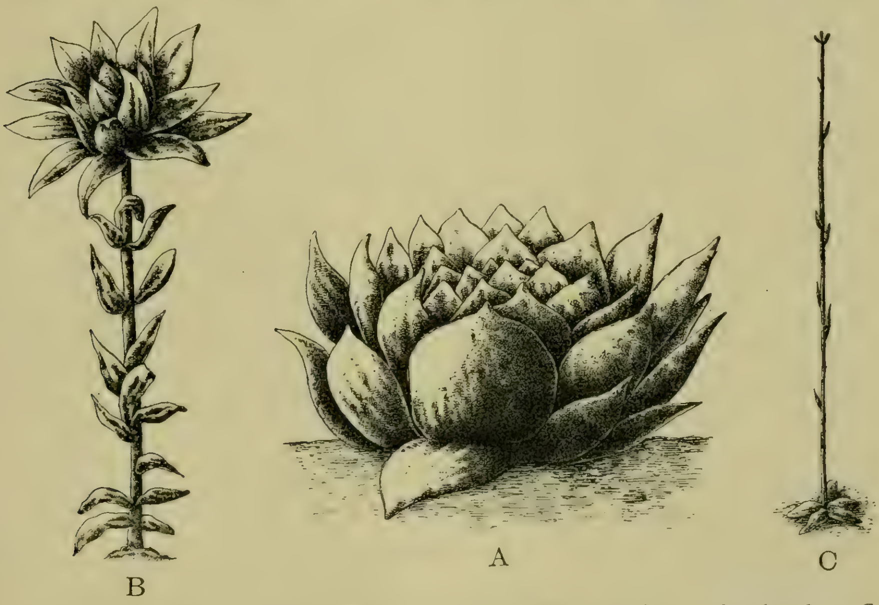

FIG. 167. *Sempervivum assimile.* *A*, normal; *B*, grown in a moist chamber; *C*, grown in a dark room. Redrawn, after Brenner.

The effort in question may be fairly interpreted as a response to the increased humidity, the increased surface offering additional facilities for transpiration.

The formation of slender cylindrical stems instead of the normal flattened "joints" seen in *Opuntia Opuntia*, *O. leucotrichia* and some other Cactaceae is not exhibited by all plants of this general character, however. Thus the leaf-like shoots of *Phyllocactus latifrons* do not lose their bilateral form and organization, although reaching a much reduced size when grown in darkness.[175] It is to be said, however, that the results in question were partly secured by "partial etiolations" and the exact limits of the groups which undergo a reduction of the bilateral features can not be determined without further investigation. It seems entirely probable that the requirements of the transpiratory functions might be quite an important factor in a group which has made such sweeping adaptations to the conditions of humidity.

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[174] Brenner, W. Untersuchungen an einigen Fettpflanzen. Flora. 87: 387. 1900.

Etiolation of Xerophytes with Reduced Leaves and Spiny, or Cylindrical Stems.—The examination of the information obtained by the etiolation of the second group of forms that have made marked adaptations to transpiratory conditions brings in some further considerations. *Asparagus officinalis* (p. 73), *Bowica volubilis* (p. 82), *Ibervillea Sonorae* (p. 197), and *Equisetum arvense* (p. 103) were cultivated in the dark room under conditions of a higher degree of humidity than that ordinarily, and continuously encountered, by three first-named species. According to the conclusions of Brenner, and the suggestions of Palladine and Wiesner the culture of these plants in a humid atmosphere should have produced a lengthening of the stems and an increase of the surfaces capable of transpiration. It was to be seen, however, that the etiolated stems of this group were in general shorter than those grown in light, the decrease in length being accompanied by accessions to the thickness. Branching was reduced in all of the species in question when grown in darkness. No extension of the surface was reached by etiolation, or as a result of it, although it is to be said that all of these forms developed stomata, and that the outer membranes were much more adapted to a cuticular exhalation of water than the normal specimens, while the bract-like leaves were actually larger than the normal. The total result could not have been to make an increase of the transpiratory capacity of the plants examined in any instance, and the conclusion is inevitable that the moisture relations of the individual must play a minor part in the determination of the stature of the shoot when acting simultaneously with the influence of light and darkness, conforming more nearly to the action of *Capsella* as outlined by Wiesner.[176]

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[175] Vöchting. Ueber die Bedeutung des Lichtes für die Gestaltung blattformiger Kakteen. Jahrb. f. wiss. Bot. **26**: 438. Also see Goebel. Organography of Plants, p. 248. 1900.

[176] Wiesner, J. Formänderungen von Pflanzen bei Cultur im absolut feuchtem Raüme und im Dunkeln. Ber. d. deut. Bot. Ges. **9**: 46. 1891.

Etiolation of Stems of Woody Perennials. — Species with woody stems which were grown in darkness in my experiments include *Acer rubrum* (p. 188), *Baccharis halimifolia* (p. 80), *Cornus alternifolia* (p. 97), *Fagus Americana* (pp. 105, 194), *Populus Simonii* (p. 154), *Quercus* sp. (p. 161), and *Rhus* sp. (p. 169) in the adult stage, and *Castanea dentata* (p. 91), *AEsculus hippocastanum* (p. 191), *Gleditsia triacanthos* (p. 113), *Hicoria minima* (p. 114), *H. ovata* (p. 115), *H.* sp. (p. 113), *Quercus palustris* (p. 158), *Q. rubra* (p. 159) and *Q.* sp. (p. 161), in the seedling, or juvenile stage. The reactions showed the greatest divergence, a part of which may be attributed to the unsuitability of the cultural conditions offered for some of the forms. Effects from such causes were recognizable to some extent, and results due to unfavorable factors may be easily eliminated in the analysis of the influence of darkness upon the growth and development of the species in question. *Fagus Americana*, as examined by myself, and *F. sylvatica* according to Jost bear a specialized relation to light and darkness of an unmistakable character. The buds of young plants might awaken in darkness in my own tests, but the buds of adult plants a few years older did not begin activity except under the influence of light. This influence was furthermore wholly of a stimulative character, as Jost found that when a few buds of a confined plant were exposed to light the stimulation resulting was sufficient to awaken others on distant parts of the shoot from which light was excluded, a result wrongly attributed by Jost to the necessity for the action of light in the construction of formative substances necessary for the development of buds. Furthermore, this reaction illustrates most strikingly the difference of results that may be obtained by total and partial etiolations. Again, this awakening of the buds only under the influence of light, and the fact that etiolated stems do not make greater growth than the normal, points most strongly to the conclusion that, in these two species at least, light does not exert a retarding, or indeed a direct action of any kind upon growth; the behavior of the plant with regard to this factor being wholly in response to its stimulative action.

A further phenomenon of marked interest in *Fagus* was the fact that both young and adult plants formed calluses rapidly in darkness, and that the buds arising from these calluses made a much more rapid growth than the normal, being capable of extension in darkness as well as in light. The typical buds showed only a slight elongation of the axis in some instances and the cessation of growth of the etiolated branches was followed by the formation of a number of loose, brownish sheathing scales around the tips of the branches.

The etiolated branches of *Baccharis* did not offer any striking differences in form or size from the normal, although the brief duration of the organs formed in darkness demonstrated that the temperature and soil conditions were not suitable for this shrub. *Acer*, *Cornus*, *Populus* and *Rhus* developed etiolated branches much longer than those on correspondent normal portions of the shoot. The length of etiolated shoots of *Acer* was about double that of the normal, an increase that was due in part to the multiplication of the number of internodes, and in part to the excessive elongation of all of these members. The number of etiolated internodes in a branch was about the same as that in juvenile sprouts arising from the bases of trunks, or from calluses on trees in the open, but the lengths of the etiolated internodes was greater than that of the juvenile members, while the thickness in the two instances were about equal, being greater than that of normal twigs on the shoot or main crown. The approximation of the etiolated and juvenile branches seems to point to the fact that the growth of branches in darkness does not allow development to proceed much beyond the embryonic condition. In one instance the juvenile condition is shown as modified by growth and development in light; in the other the embryonic stage is continued under the influence of darkness. The endurance of the etiolated twigs corresponded fairly well with the length of an ordinary growing season, but the terminal buds did not continue activity during the entire period, since most of them soon perished, and lateral buds took up the continuation of the branches. It is notable, however, that none of the etiolated branches succeeded in making such development as to pass into permanent form and to survive after the leaves had perished. Buds of *Acer* awakened but tardily, and in less number on trees in darkness than in light, and exposure to illumination seems to exercise a stimulative effect on the awakening of the growing points. It was noted that even the occasional exposure to the rays of the electric lamp used in making examinations of the etiolated specimens produced some reaction in the way of increased development of the buds. The length, diameter, and number and length of internodes of stems of *Cornus* grown in darkness were much greater than those of normal branches on correspondent portions of the shoot or crown, being approximately the same as in juvenile sprouts arising from the base of trunks. The etiolated branches failed to develop beyond a certain young condition although their existence extended over a period of five months, which is fully equal to the entire vegetative season of the tree. None of the branches grown in darkness succeeded in accomplishing such differentiation and development of tissue as to allow them to pass into permanent form, all of the etiolated twigs dying back to the old stems at the end of their period of activity. Unlike *Acer*, branching occurred with normal frequency, but the branches, both primary and secondary, assumed an erect attitude in darkness, due to an alteration in the geotropic properties, or to the lack of the phototropic stimulation in response to which the branches habitually assume an approximately horizontal position in light.

The length, number and length of internodes, and diameter of etiolated branches of *Populus* were greater than in normal branches, no comparison having been made with juvenile sprouts. The primary branches assumed a position approximately horizontal in some instances, and the secondary branches which were produced in some profusion were more or less nearly erect. The branches grown in darkness were of comparatively brief duration and did not succeed in making such development of tissues as to pass into permanent form, dying back to the base in a few weeks.

The etiolated twigs of *Rhus* did not exceed the normal in length, number and length of internodes, or diameter. No branching was observed in the single specimen grown in the dark room, and the blanched members soon perished, their duration being much less than that of a vegetative season.

The records of etiolations of entire trees by previous investigators are extremely meager. J. A. Hill writes in 1759: "The growth of plants, at least their regular growth, as well as their absolute life depends not only on warmth and moisture, but on light; this moves their juices, and upon this motion greatly depends their increase. If tender plants be kept in constant darkness they lose their leaves and die. Thus Mr. Lee, of Hammersmith, at my desire, making the experiment most fairly, killed two tamarind trees and an abrus; and would have killed an erythrina, but he gave it light in time and recovered it. Light keeps the juices in motion; and this preserves the whole. When it is not admitted these stagnate, and they ferment soon after; then the part falls off, and the plant, wanting its necessary organs, perishes."[177]

Nearly all tests with the larger woody plants have been made by "partial etiolations," which have been shown to secure results wholly unlike those from complete exclusion from illumination. The observations made by Jost on *Fagus*, are the only authentic instances in which proper methods were used, and his work showed most conclusively that the action of light was necessary to awaken the buds of this tree. It is not unlikely that the temperature may be an important factor in awakening the activity of the buds of trees, and that the species examined by myself might show greater activity at the unknown optimum temperature in darkness. So far as the actual facts are at hand however, the conclusion seems warranted that the buds of *Acer*, *Cornus* and *Fagus* are stimulated to activity by the action of light, and that only a small proportion of the normal number may grow in darkness. *Populus* seems capable of carrying out the activity of its buds to a much greater extent than the other species in darkness. Etiolated branches do not advance beyond an embryonic condition, and do not form permanent tissue, enduring over a period not greater than that of an ordinary vegetative season. No previous discussion has been made of the fact that all woody plants showed a tendency to develop buds on the basal portion of the shoot in darkness, the terminal portions awakening tardily and only in small numbers, proving very refractory in darkness, although appearing sound and healthy after continued confinement in the dark room. Seeds of these woody plants germinated quite as readily in darkness as in light, the stems formed in darkness being longer than those grown in light, but in no instance were branches formed or the lateral buds awakened except upon the destruction of the terminal bud of the main stem. The stems of etiolated seedlings of this class were longer and thicker than those of normal plantlets, and the internodes were longer, the number of the latter not being increased in all instances. The etiolated stems of seedlings showed marked variations from the normal in the manner of development of the phellogen and generative layers. A further notable feature of the etiolated stems of woody seedlings consisted in the fact that the basal portions of the main stems contained more or less permanent tissue. When the terminal portion of the stem perished, lateral buds near the base would awaken after a resting period and carry out a second season's growth, when death finally ensued from a concurrence of causes of which deficient nutrition must have played an important part.

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[177] Hill, J. A. Anatomy of plants, p. 213. 1759.

Etiolation of Stems of Herbaceous Biennials and Perennials.— The greatest amount of observation and experiment upon etiolation has been made with herbaceous species in which the aërial stems are sent up from subterranean axes containing more or less storage material. The species examined by myself are as follows: *Aster divaricatus* (p. 78), *Botrychium obliquum* (p. 80), *Brassica campestris* (p. 84), *Cypripedium montanum* (p. 101), *Delphinium exaltatum* (p. 102), *Galium circaezans* (p. 106), *Hydrastis Canadensis* (p. 117), *Hypopitys Hypopitys* (p. 119), *Ipomœa Batatas* (p. 120), *Lysimachia terrestris* (p. 123), *Pastinaca sativa* (p. 143), *Phytolacca Decandra* (p. 149), *Podophyllum peltatum* (p. 150), *Saururus cernuus* (p. 179), *Solanum tuberosum* (p. 180), *Trillium erythrocarpum* (p. 181), *T. erectum* (p. 182), *Vagnera stellata* (p. 185) and *Viola rostrata* (p. 187).

Hypopitys Hypopitys differs from the other species treated under the above heading in the fact that it derives all of its construction material from underground organs consisting of roots symbiotically organized with mycorrhizal fungi, in consequence of which it has undergone most sweeping morphological degenerations of the stelar tracts and members of the shoot and root-systems. The degeneration of the tissues has been accompanied by a loss of the capacity for reaction to the direction of rays of light by phototropic movements. Furthermore, it has been found that light is without appreciable effect upon the shoot, the specimens grown in darkness not differing appreciably from those in light. Some fungi were seen to make excessive elongations of the sporophores in darkness, while others were unaffected. It is difficult to assign an explanation for such divergence of reaction among forms of supposedly similar physiological organization.

A large number of herbaceous species of this group including *Aster divaricatus*, *Cypripedium montanum*, *Galium circaezans*, *Ipomœa Batatas*, *Phytolacca Decandra*, *Saururus cernuus* and *Vagnera stellata*, do not make any excessive elongation of the stems or shoots in darkness. Stems of these species developed about the normal number of internodes in darkness, which did not exceed the usual length, except in a few instances in which the basal ones were slightly longer than the corresponding members of normal stems. The upper internodes failed to reach the normal length by such amount in stems showing this reaction, that the ordinary length of the axis was not exceeded. In some species etiolated stems were thicker than the normal, due to exaggerated development of cortical or parenchymatous elements, both in size and number, and the angular contour was more or less completely lost, the tendency being shown toward an isodiametric section. The advance from the embryonic condition reached various stages, but in no case was the differentiation and construction of the elements completely normal. The primary annular and spiral vessels approached the normal in structure perhaps more nearly than any of the elements, but these generally showed altered dimensions of the lumina with thinner walls. Tissues with purely mechanical functions were more reduced than other forms. The rigidity of the etiolated stems was thus dependent upon the turgidity of the delicate and incompletely formed tissues, and they were consequently fragile and easily damaged by bending or mechanical contact. Branching was not shown to any extent and the shoot was seen to consist of a single stem bearing the reduced leaves. In some instances basal branches ordinarily having a propagative function were produced, and if *Solanum* might be included, it may be said to be the only species capable of forming reproductive bodies of any kind when etiolated. It is to be seen by reference to page 222 that the reactions of the climbers agree with those exhibited by the species included in the above group.

Exaggerated elongations of the stem are shown by *Botrychium obliquum*, *Brassica campestris*, *Delphinium exaltatum*, *Hydrastis Canadensis*, *Lysimachia terrestris*, *Pastinaca sativa*, *Podophyllum peltatum*, *Trillium erectum* and *T. erythrocarpum*, and *Viola rostrata*. The excessive growth to which this elongation was due was variously distributed. Exaggerated growth in length took place in all of the internodes of *Brassica* and *Lysimachia*, and throughout the entire stalk of *Hydrastis*. The basal internodes of *Delphinium* and *Viola* were most elongated, although some excessive lengthening occurred in all of the stems, while in *Botrychium* the increase over the normal was found entirely in the upper part of the stalk, the lower portion being somewhat shorter than the average. Branching was much reduced from the normal habit. The development and differentiation of the tissues of the species of this group reached a much more advanced stage than those of the preceding group, and the period of endurance or existence of the etiolated stems consequently was as great as in the normal, in many instances. Etiolated stems were distinguished from the normal by having less angularity, but no species of this group showed etiolated stems of greater diameter than the normal.

Species having the largest amount of reserve food stored in the perennial portions of the plant might be expected to be capable of carrying on a relatively greater development of the stem in darkness, or under any conditions in which the plant is forced to rely upon its own supplies or activities. As a matter of fact not all species are capable of carrying on growth and construction to the full value of the food supply. A few species, notably the seedlings of *AEsculus* exhibit this capacity and doubtless many others might be found; hence nutrition must be the limiting factor in the development of many species in darkness. On the other hand, the shoots of some species perish, although ample and copious supplies of reserve material remain intact in the storage organs. In such instances it is seen that the difficulty may lie in the difficulty of transporting the food-material to distant parts of an elongating shoot, which customarily construct much of their carbohydrates locally, by means of conduction tissues which are much reduced in cross section and which, in common with other specialized tissues, have failed to reach normal differentiation. In order to give the evidence bearing upon the matter of ability to utilize the entire reserve greater conclusiveness, it would be necessary to make a special series of tests in which the requirements of the species when etiolated, as to moisture and temperature would be quite exactly complied with, and the activity of bacterial and fungal organisms upon the storage organs was checked. In so far as defined above therefore, nutrition must be taken as important factor in the divergences of etiolated plants from the normal. It is not clear, however, that nutrition is a major factor in the process, as asserted by Sachs,[178] who said: "Moreover, the size of a plant developed in the dark, as well as the number of roots and leaves formed, are proportional chiefly to the volume and mass of the seed, or better, to the quantity of reserve materials accumulated in it." "At length, however, after a few days, or in the case of very large seeds, after a few weeks, the growth in the dark always ceases, and the whole plant become diseased and perishes; in many cases, as with *Phaseolus*, etc., not until all the reserve-materials of the seed have been completely used up for the formation of organs; in other cases, however, as with the gourd, growth and the development of organs cease while the cotyledons still retain considerable quantities of unused formative substance." My own experiments lead to the conclusion that etiolated growth is indeed not possible beyond the capacity of the stored formative substance, but the ability of the plant to use all of this material depends upon other factors, which are in fact the principal causes to which the characteristic form of etiolated plants is due. Without further discussion of these causes at this time it may be regarded as quite well founded that the death of etiolated seedlings, or adult plants in darkness, is generally due to the incapacity of the imperfectly differentiated conducting tissues, or to the destruction of the reserve-material by disintegrating or fermentative processes. The development of the transpiratory system must also be taken into account in the consideration of the mechanisms for translocation of material in the plant.

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[178] Sachs. Physiology of Plants. p. 531. 1887.

Influence of Etiolation on the Development and Differentiation of the Tissues and Emergences. — The meager facts recorded, concerning the effects of darkness and light upon trichomes, in my own observations are not sufficient to furnish a basis for any generalizations upon this subject, and previous investigations have been made under various conditions of imperfect and partial etiolation. Hairs are ordinarily present on the aërial stems of *Apios*, but were lacking from etiolated stems, although present in subterranean shoots, which the stems grown in darkness resembled in some particulars (see page 42). Etiolated hairs of *Hydrastis* were only about one-fourth of the size of the normal both on the stem and leaves, although the former was unduly elongated and the latter reduced. The stalked glands of *Lysimachia* were unchanged on stems which underwent excessive elongation, and did not appear so numerous in *Menispermum*, although of about normal size. The hairs of *Populus* were smaller than the normal, although the other epidermal elements were much elongated. No marked alterations could be seen in the hairs of *Aster*, *Cornus* or *Fagus*, although the first two species exhibited excessive elongations of the stems on which these structures were borne. The prickles of *Smilax* were both more slender and shorter on etiolated stems than on normal plants. It is to be seen, therefore, that the conclusions of Schober that the reaction of these structures is correlated with the habit of the member on which they are borne are not sustained (see page 22).

Development of Stomata on Etiolated Stems. — The development of stomata was likewise subject to great variation among the different species examined, and an intimate connection was found between the degree of development of the leaf or stem, and the differentiation and number of these organs. Stomata were present on the stems of *Apios*, *Asparagus*, *Bowiea*, *Hydrastis*, *Lysimachia*, *Menispermum*, *Opuntia* and *Phytolacca*, but as no special record was kept of this feature it is probable that they might be found on many other etiolated stems. Furthermore, the simple fact of the occurrence of stomata on any etiolated stem is of importance only when similar data have been obtained from normal stems, and this was neglected in my observations. So far as a general inspection of the results may be taken to be of value, stomata appeared to be most numerous on etiolated stems capable of long duration and extended development in darkness, although shoots that were capable of formation of foliar expansions sometimes showed stems entirely lacking these organs. It is notable that no stomata were found on the etiolated aërial stalks of *Podophyllum*, and that the stomata on the stems of *Viola rostrata* failed to open. Only a small proportion of the entire number of prestomatal elements passed into the final stage in *Phytolacca*, and the stomata on the cylindrical etiolated shoots of *Opuntia* were much reduced in size.

Lenticels of Etiolated Stems. — Lenticels appeared to be more numerous, especially on the basal portions of stems of etiolated seedlings of *Acer*, and *AEsculus* than on normal seedlings, and lenticellar formations were also more abundant on the lower portions of the etiolated stems of *Ibervillea* and *Smilax* than in the normal. On the other hand, lenticels normally present in *Populus* did not develop beyond the first stage in etiolated stems (see Fig. 117). Structures of this character were to be seen in great number on roots of *Cocos*, but it could not be said that an abnormal number had been produced, for no exact comparisons could be made. No generalizations may be made as to the behavior of these organs with respect to light and darkness in view of the insufficient data at hand.

Epidermal Cells of Etiolated Stems. — Epidermal cells were found to be as long as the normal in all instances, except in *Menispermum*, in which species alone the superficial measurements were less than in normal stems. The epidermal cells showed an increase in all dimensions in a great number of instances in which a multiplication of these elements had also ensued. Among the earlier investigators various contentions arose as to whether the excessive elongation of stems was accompanied by increase in size, or by increase in number of the epidermal cells, the conclusions of the various workers being based upon the small number of species examined. It is to be seen however, that no general law has been discovered by which the action of the epidermis in darkness may be predicated.

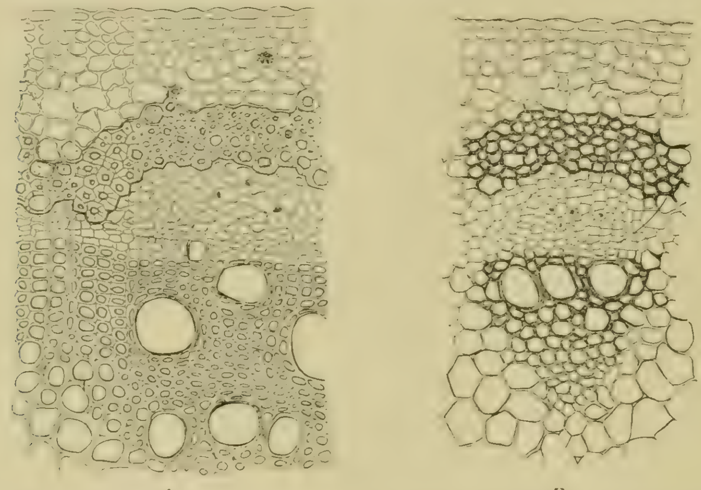
A. *B.*

FIG. 168. *Polygonum cuspidatum.* *A*, partial transverse section of normal stem; *B*, partial transverse section of etiolated stem. After Rauwenhoff.

In so far as the mechanical features of the epidermis are concerned it is to be said that these elements, without exception, either in my own work or in the experiments of previous investigators, fail to attain the thickness of wall and the consequent mechanical rigidity of the normal. The lack of thickening is most noticeable with respect to the outer wall, and the ordinary cutinization and deposition of secretions has not been observed in any of the species examined by myself. The end walls show a tendency to lie more nearly parallel to the circumference of the stem. The epidermis, in common with many other tissues, does not advance beyond a certain primary stage of development, and retains the power of growth and division in the cells during a much longer period than in the normal plant; consequently it can respond to stresses and other factors, which may cause it to undergo increase in size, alterations in form, or multiplication of the cells by division. Thus the epidermis is compelled to make adjustment to the augmented diameter which some stems attain by increase in bulk of the cortical and medullary tracts.

Collenchymatous Layers in Etiolated Stems. — Collenchyma shares with other mechanical tissues in a general reduction which, in some instances, amounts to a total disappearance from etiolated stems. The collenchymatous layer ordinarily underlying the epidermis failed to appear in etiolated stems of *Galium* and *Menispermum*, and consisted of a tract of tissue with cells reduced in number, or thickening of the walls in *Aster*, *Saururus* and *Viola*. *Phytolacca* offers the single exception of the formation of this tissue in a manner approaching the normal in etiolated stems. The subepidermal layers generally shared the enlargement of lumen and lessened thickness of wall that was to be observed in the cortical tissues of the greater number of species examined. It seems justifiable to conclude therefore, that collenchymatous tissue is not affected in its development by light and darkness directly, but that the differentiation of this tissue is due entirely to secondary causes dependent upon the phenomena included in the growth and development of the tissues interior to it.

Formation of Periderm on Woody Etiolated Stems. — The epidermal and cortical tissues of the trees examined in my experiments offer three types of reaction. Branches of *Populus* grown in darkness were characterized by the failure of the tissues to develop beyond an extremely simple stage and the cortex was composed of elements which were larger, and with thinner walls than in the normal, while they were variously distorted from the somewhat regular form of the normal elements. The differentiation of the cortex into an outer and inner region was wholly lacking. No activity of any kind was to be found that presaged the formation of bark. In a second type the behavior of the tissues involved only comparatively unimportant departures from the normal. This procedure was seen in *Acer*, although differences due to lack of thickening in the walls of the epidermis, collenchyma, and cortex were to be seen. The elements of the latter were compressed radially. A similar state of affairs was to be seen in seedlings of *AEsculus*. Perhaps the least variation from the normal was to be seen in branches of adult trees of *Fagus* grown in darkness, in which the phellogen, epidermis, collenchyma and cortex were present in an order differing from the ordinary forms only by a lessened thickening of the walls of all these tissues. In *Cornus* the cortical cells showed abnormally large measurements in all radii with a lessened thickening of the wall, while the epidermal cells began to collapse earlier than in the normal, the underlying tissues also being less thickened. This was accompanied by a precocious development of the phellogen, which however had much the normal structure and arrangement. The most striking departures from the ordinary formation of bark were offered by the various species of *Castanea*, *Hicoria* and *Quercus* constituting the third type. The seven species brought under observation agreed in the normal formation of phellogen in the epidermal region. In etiolated specimens of *Castanea* and *Hicoria* the epidermal cells remain intact for some time, and a layer of cortex in the median region in *Hicoria*, and about in the locality of the collenchyma in *Castanea* begins to collapse (p. 93). Internal to the collapsing layer, and sometimes in contact with it in *Hicoria*, an abnormal layer of phellogen was formed. The cortical cells of plants of this group showed no increase in size or marked changes of form outside of those consequent upon the above alterations in behavior of the bark-forming tissues. The walls of these elements were less thickened than in the normal, and fewer crystals might be seen than in the normal. The procedure described above has the effect of reducing the external diameter of the portion of the stem in which the action takes place, in consequence of which the stems are smaller at the base than the normal, or than the upper, younger portions of the same stems. In *Quercus* the epidermal and subepidermal regions collapse early in the development of the stem. Ordinarily the epidermis endures for a long time and a phellogen is formed immediately underneath, consisting of eight to ten layers of cells. The cells which usually undergo collenchymatous thickening internal to the phellogen seem to be involved in the collapse, and a median layer of the remaining cortex gives rise to a phellogen consisting of several layers of cells. The cortical elements appear larger in all dimensions than in the normal. The collapse of the epidermal and outer cortical cells begins with the outermost layer and extends inward slowly, having the final effect of reducing the thickness of the portion of the stem affected even more than is done by the similar process in *Hicoria* and other species. The difference in diameter between the base of an etiolated stem and the portion a few centimeters above it is often very great comparatively.

Bast Fibers of Etiolated Stems. — The extended periods over which the plants used in my own experimental tests were observed gave much better opportunity for the examination of the behavior of the bast fibers than have been enjoyed by any previous worker that has dealt with this subject. The differentiation of this tissue was but slight in *Apios*, *Acer*, *AEsculus*, *Aster*, *Castanea*, *Cornus*, *Fagus*, *Falcata*, *Lysimachia*, *Menispermum*, *Populus* and *Quercus*, and but little thickening occurred in the walls, although some of the species in this group develop stems in darkness that continue growth for several months. On the other hand, the species of *Hicoria* that were cultivated in the dark room carried the development of the bast fibers to an advanced stage, although corresponding to *Castanea* and *Quercus* in the general activity of the cortex, epidermis and phellogen. So far as other features are concerned, a general inspection of the structure of the etiolated stem of *Hicoria* and *Quercus* does not show that the woody tissues of the former are carried beyond those of *Quercus*. Development and differentiation of the bast fibers may be carried on in etiolated stems, but as stated above it occurs in but few species.

Endoderm, Pericycle, Sieve Tissue, Cambium and Generative Layers of Etiolated Stems. — The numerous questions connected with the origin and occurrence of the endoderm and pericycle made it impossible to carry out a critical study of these formations in the time at the disposal of the author, and but little study was made of the sieve cells in the various stems. The last-named tissue seemed to be differentiated but slightly in most of the etiolated stems, so far as the records at hand may be relied upon. The following striking facts concerning the activity of generative tissues may be cited at this place. A distinct cambium is not normally formed in *Apios*, the stem soon ceasing to increase in thickness in light. Etiolated stems however show a diameter greater than the normal, and a generative layer arises in the customary position of the cambium, while a second is formed in the pericyclic region, which is about half the thickness of the primary generative layer. A marked cambium was present in etiolated stems of *Castanea*, *Fagus*, *Hicoria* and *Quercus*. *Phytolacca* formed the first of the secondary layers of cambium characteristic of this plant, when grown in darkness. The differentiation of cambium is of course closely connected with the general advance of the stele from the embryonic stage, but it is difficult to connect its development with that of any single tissue in the species used in the tests.

Effect of Etiolation on the Stele.—The walls of the elements of the xylem were less thickened in the etiolated than in the normal stem. In some instances the lumina of the vascular elements were smaller than the normal, in others no noticeable difference from the normal size was to be made out, and in a few, of which *Quercus* is an example, the lumina of the vessels were greater than the normal in cross-section. The inter-fascicular parenchyma, and the thin-walled cells throughout the xylem were smaller in etiolated stems than in the normal, while the pith or medulla attained at least normal bulk and were generally greater than in normal stems. The increase of this tissue has led many investigators to attribute the altered dimensions of etiolated stems to be due to its direct action as a cause. The central parenchymatous mass of a stem however, is seen to continue growth and perhaps multiplication of the elements during the embryonic stage, and if this is lengthened by any cause such as etiolation, the natural increase of the parenchyma would lead to the increase of the bulk of the stem by its unchecked action. The polystelic stems examined increased notably in diameter as a result of etiolation, the added bulk being largely made up of parenchymatous elements, and the central lysigenous splitting did not always occur, as was found in *Asparagus*.

A consideration of the reactions of the various tissues of the stem in darkness fails to detect a single universal and invariable reaction on the part of any tissue, except perhaps in the lessened thickening of the cell-walls that is found in all of the external regions of the stem. This lack of deposition of aplastic matter is very clearly a matter of continued growth and development of the etiolated axis, and is not a direct response to darkness or the absence of light. The behavior of the etiolated stem is, therefore, not reducible to its first cause by an analysis of the activity of its constituent tissues, although an examination of the components of the stem indicate the general nature of the etiolative reaction. The continued simple growth made by the plant, unaccompanied by the customary morphological development and differentiation of the tissues, may be taken to account for all of the anomalous structures of plants grown in darkness. The general relation of this condition to light and darkness will be taken up in the latter part of this paper.

Etiolation of Leaves.—The observations of the behavior of the stem in darkness showed a uniform reduction of the branches of the main axis of the shoot, but this decreased volume, and extent of the ramifications of the stem was not seen to extend to the foliar members of the shoot. It will be found most convenient to take up these organs in groups according to their morphological character and the general habit of the plants concerned. An observance of these distinctions leads to the separation of the foliar organs of pteridophytes into two groups, viz., sterile and spore-bearing leaves.

The etiolated leaves of *Lycopodium lucidulum* attained less than a half of the normal size and were slightly tinged with green, due to the presence of chlorophyl, which was present in but minute quantities. An erect position was assumed (p. 199). *Asplenium platyneuron* (p. 75) developed excessively elongated leaves in darkness by an increase throughout the entire rachis, and the pinnae were in consequence much more widely separated than in the normal. The pinnae were expanded, but had a superficial area much less than the normal and were more irregularly cut and incised than the normal, the basal auricled lobe being present in modified form. The mesophyll was but slightly differentiated and the other tissues of the leaf were also in an incomplete condition. Stomata were present, and apparently functional, although not so large as in the normal. The entire leaf was greenish from the presence of chlorophyl. Etiolated leaves were apogeotropic, but fell over as soon as a length of a few centimeters was reached with the result that the tips soon curved upward. Fully etiolated and extended leaves were capable of some further growth and development when illuminated. No trace of sporogenous tissue could be found on the pinnae. The stipes of *Botrychium* (p. 80) underwent excessive elongation in darkness, the unusual growth occurring in the upper portion, and also in the basal portions of the stalks of the pinnae. The etiolated stipes were of greater diameter than the normal, and enough chlorophyl was present to give the entire aërial portion a decided greenish tinge. Stomata were present and functional. The epidermal cells were excessively elongated in a degree correspondent to the increased length of the stipe. The laminar rudiments remained in close clumps in an undeveloped condition. The customary thickening of the walls of the epidermal and other tissues did not ensue, and the stele did not develop beyond a primitive stage, although the etiolated leaf lived for a period of many weeks. *Pteris longifolia* (p. 157) showed an exaggerated elongation of the entire rachis in such manner that the distance between the pinnae was increased one-half above that of the normal. The thickness of the rachis was greater than in the normal, due to an increase in the parenchymatous tissues, and the entire organ contained some chlorophyl. The pinnae did not attain a size beyond one-sixth of the length of the normal, not being entirely unfolded, and were held in various abnormal positions. The leaves assumed an erect apogeotropic attitude, sometimes falling over by their own weight. *Woodwardia radicans* (p. 188) produced a succession of leaves after the manner of some of the seed-plants, none of which developed stipes much longer than the normal. The laminar rudiments remained in an unfolded condition in tightly rolled clumps, the entire leaf containing some chlorophyl.

Two species of ferns were examined in which the sporophylls are specially differentiated organs, and the leaves are entirely sterile, viz: *Osmunda cinnamomea* (p. 132) and *Polystichum acrostichoides* (p. 151). *Osmunda* showed an exaggerated growth of the stipe and rachis. The pinnae were pinnatifid in etiolated specimens, the divisions being fully expanded and the entire leaf was green from the presence of chlorophyl. The etiolated organs were apogeotropic but soon fell over by reason of their weight and great length. The mechanical tissues of the epidermal region were but slightly developed and the steles did not advance beyond an early or incomplete stage of differentiation. The reduction was also marked in the endodermal and pericyclic regions. Etiolated leaves of *Polystichum* underwent an exaggerated elongation of the basal portion of the stipe, especially while some increase was shown by the entire rachis. The pinnae remained rolled up in small clumps, being separated more widely than in the normal. No development of the sporophylls ensued, the stimulating action of light being apparently necessary to start them into activity. The normal leaves of *Polystichum* assume a decumbent position more or less closely approaching the horizontal, while etiolated organs are strictly erect. When etiolated leaves were illuminated however, the upper portion of the rachis, bearing pinnae, was brought to a position approximately horizontal by an abrupt curve in the petiolar stalk immediately below the basal pinnae. The pinnae also were capable of some development under these circumstances. Etiolated leaves contained some chlorophyl.

Etiolation of Leaves of Monocotyledons with Parallel Venation. — In the greater number of species of this type examined, the axis of the plant consisted of an underground tuber or rhizome, the leaves arising from the axis and being held in a position variously approximate to the vertical. A few instances came under observation in which the leaves were borne on aërial stems. The species included in the group in question are: *Allium Neapolitanum* (p. 37), *A. vineale* (p. 39), *Camassia* (*Quamasia*) (p. 87), *Erythronium Hartwegi* (p. 104), *Hemerocallis* (p. 113), *Hyacinthus* (pp. 116 and 117), *Iris* (p. 121), *Narcissus Tazetta* (p. 128), *Ornithogallum umbellatum* (p. 130), *Sansevieria Guineensis* (p. 171), *Sparaxis* (p. 180), *Tipularia unifolia* (p. 181), *Aplectrum spicatum* (p. 46), *Tritelia uniflora* (p. 182), *Tulipa* (p. 185). Many of these bore leaves in darkness which attained a length, and sometimes also a breadth, in excess of the normal and a superficial expansion equal to, or greater than, that of normal organs. The leaves of *Allium* and also those of *Quamasia* were of a size approximately normal, although variously distorted from the usual stature and position. The leaves of *Aplectrum* and *Tipularia* were longer than the normal, though of diminished width and the bracts at the base of the inflorescence axes were unduly elongated, with the width of organs grown in light. The leaves of *Erythronium* showed but little alteration. The leaves of *Hemerocallis* did not attain a size equal to that of the normal and those of *Hyacinthus* were longer than the normal, being rolled and twisted, but showing a width not much less than the normal when extended, an observation also made by Sachs, who describes etiolated leaves of *Allium Cepa* and *A. Neapolitanum* as being longer than the normal and lacking the central lysigenous cavity. *Iris* produced etiolated leaves of a length in excess of the normal. The greatest increase of etiolated leaves above the normal has been found by several observers to be shown by *Narcissus*, in which a length of three or four times the ordinary measurements has been seen. Such organs are described as slightly narrower than the normal by most observers, and the lysigenous cavity in the center diminished in volume. In the examples that came under my own observation however, the blades were of full average width. Etiolated leaves of *Tritelia* or *Milla* were two or three times the length of organs grown in light, and also showed a slight increase in width. The curvatures and torsions present, to some extent, in green leaves were accentuated in etiolated organs, becoming most pronounced as maturity was reached and death set in. The two species of *Tulipa* examined developed leaves, the margins of which had inrolled margins and marked torsions were shown. No comparative measurements were made, but an inspection of the etiolated leaves suggests that an abnormally large size was reached. Stomata were seen in etiolated leaves of *Allium*, *Aplectrum*, *Hyacinthus*, *Iris*, *Narcissus*, *Tipularia*, *Tritelia* and *Tulipa*. It may be said that leaves of the above species arising from subterranean bulbs or stems attained normal or supra-normal dimensions with open, and probably functional, stomata in all instances, although this last statement does not rest upon exact observation, and have a duration fairly equal to that of the normal under ordinary circumstances. The normal green leaf would doubtless prove more resistant under unfavorable circumstances and under prolonged seasonable conditions would live longer than etiolated leaves. The fact stands out prominently that torsions and curvatures naturally present in some species are accentuated, and are also shown by species not usually exhibiting such phenomena. The positions assumed by many etiolated leaves of this group are due in greater part to the direct action of curvatures and torsions arising autotropically rather than to any positive reflexive action. Leaves of *Aplectrum*, *Bowiea*, *Camassia*, *Hyacinthus* and *Iris*, were held in an erect position until they perished; although no geotropism was directly demonstrated, yet it seems justifiable to assume the capacity of such reaction. On the other hand, the leaves of *Allium*, *Narcissus*, *Ornithogallum*, *Tipularia*, *Tulipa* and *Tritelia*, were held in various prostrate and decumbent positions. The terminal portions of the leaves of *Narcissus* and others occasionally curved upward. The curvatures and torsions noticeable in some of the leaves, as well as in many etiolated stems, are perhaps due in part to the exaggerated inequalities of growth consequent upon the prolonged continuation of the activity of tissues in an embryonic condition, which permits some, especially parenchymatous tissues, to attain abnormally large volume, thus disturbing the customary mechanical relations of the separate tracts. The proximity of the embryonic cells proper to the base of the leaf and to the supply of reserve food, must also play a part in the excessive growth of these organs.

Etiolation of Petiolate Leaves of Monocotyledons with Open or Reticulate Venation. — The behavior of monocotyledonous leaves arising from subterranean stems or storage organs, in which an expanded lamina was supported at the end of a distinct petiolar structure offered marked divergences from the reactions of leaves of the preceding type. The species included in this group are *Amorphophallus Rivieri* (p. 40), *Arisaema Dracontium*, *A. triphyllum* (p. 50), *Peltandra Virginica* (p. 144), *Trillium erectum* (p. 182), *T. erythrocarpum* (p. 181), *Caladium* (p. 85), *Calla* (pp. 86, 87) *Canna* (p. 88) and *Cocos nucifera* (p. 95). Of these *Amorphophallus* offers the most striking reaction since the leaves, which normally awaken upon the maturity of the fruit, or shortly afterward, did not begin growth during the entire twenty months the plants were confined to the dark room. The failure to grow might have been due to one of two causes. The temperature, which was about 20° to 22° C. during a part of the period, might have been too low, or the stimulative action of light might have been necessary to awaken these organs. An exact analysis of the matter might be made only under the environmental conditions of the native habitat of the plant. Numerous specimens of the two species of *Arisaema* were brought under experimental conditions and, in all instances, made an exaggerated growth of the petioles, while the laminar portions remained in a rudimentary condition with a volume not more than two or three times as great as when in the bud. The laminar tracts remained variously folded, and in positions determined altogether by the relative activity of the scarcely differentiated tissues. The non-development in this species is very clearly not due to lack of nutrition, since plants confined to the dark room were capable of making four successive growths of leaves in as many seasons at the expense of the food-material in the corms. Furthermore, the structure of the petioles was not so widely divergent from the normal as in petioles of dicotyledons and it seems fairly probable that the question here becomes one of stimulation rather than of direct nutrition in the development of the laminae. The etiolated leaves of *Caladium* and *Colocasia* developed petioles which were much longer than the normal, and laminae with an extension of surface less than the normal, being only partially unfolded from the rolled position of the young organ (see Fig. 41). Although the utmost care was exercised in the use of the lantern in the examination of etiolated specimens yet the few minutes' exposure to which leaves of *Caladium* and *Colocasia* were subjected during every week led to the formation of some chlorophyl in the laminae, or rather it was to be seen in fully etiolated organs. The possibility is not excluded that this substance had already been formed in the buds previous to confinement in the dark chamber. The fact remains however, that this species is able to construct chlorophyl after a very limited illumination, and this statement may be held true whether the green color was the result of the stimulation from the faint artificial illumination in the dark room, or whether it was formed as a result of the action of light upon the unopened buds. A long succession of leaves was produced on plants kept in the dark room, as has been previously described. The separate members were of shorter duration than the normal organs although furnished with functional stomata. *Arodes* (*Calla*, p. 86) produced etiolated leaves which shared the characteristics of *Caladium* in the matter of the production of chlorophyl, and in the duration of these organs. A succession of leaves was produced in darkness until the corm was more or less nearly exhausted. In this species, however, the laminae did not unroll and remained in a compact cylindrical mass, held in an erect position, while the laminae of *Caladium* and *Colocasia* were placed in various attitudes. *Calla palustris* (p. 87) developed petioles of a length slightly in excess of the normal in etiolated specimens and the laminae were expanded to an extent that approached the normal stature except that the margins were inrolled. The cultural conditions provided were evidently not suitable for this species and nothing may be deduced from its endurance, or failure to produce more than one or two leaves in darkness. Leaves of *Canna* grown in the dark chamber developed an excessively elongated petiole, and a narrow lamina which was partially unrolled in some instances, while in others it was fully expanded being held in an erect position. A succession of these organs was produced for four or five months until the material in the rootstocks was exhausted. The sheathing basal portions of leaves of seedlings of *Cocos nucifera* grown in darkness were elongated and more closely sheathing than in the normal plantlets. The laminar portions were expanded but were narrower and shorter than the normal, being held in an erect position. Etiolated leaves were capable of an existence of a year or more in darkness. The ample supply of reserve material still available in the endosperm demonstrated, that in such instances the development of the leaf was not primarily, or directly, due to lack of constructive material, although some influence might be ascribed to the failure to make such material locally. *Peltandra* (p. 144) developed leaves in darkness the petioles of which were not much longer than the normal and were somewhat thinner. The laminae were only partially extended, being much smaller than normal organs. Functional stomata were present but the leaves were of briefer duration than others grown in light. The etiolated leaves of *Trillium* (pp. 181, 182) did not attain normal expansion, the sessile laminae being held in an appressed position around the terminal flower bud. The tests of the two species of this genus were made under somewhat doubtful and faulty conditions, however.

It is to be seen that leaves of monocotyledons with an open, netted, or feather arrangement of the veins do not expand the laminar portions during growth in darkness, and that the petioles when present are excessively elongated. Sessile leaves, as in *Trillium*, do not undergo any undue lengthening of the basal portions of the laminae. The striking difference in behavior between these plants, and the species bearing leaves with a strictly parallel arrangement of the veins suggests that the amount of growth accomplished by leaves of monocotyledons arising from plants confined in darkness may be dependent upon the location of the growing zones, and upon the mechanical position of the tissues in which an abnormal differentiation and development takes place. It is evident however, that no generalizations may be maintained as to the behavior of leaves of monocotyledonous plants as distinguished from dicotyledonous forms, since the reaction of any leaf to darkness seems to depend upon structural causes to some extent, and is not conformable to any phylogenetic features of the species involved. This is further illustrated by the influence of darkness upon various types of leaves of dicotyledonous plants.

Effect of Etiolation on Leaves of Dicotyledons. — A group of species in which the leaves arise from subterranean stems or bulbs offer sufficient similarity in the more general features to warrant a separate consideration. The following may be included: *Bicuculla* (p. 80), *Cicuta* (p. 93), *Cyclamen* (p. 100), *Hydrastis* (p. 117), *Oxalis* (pp. 137, 141), *Pastinaca* (p. 143), *Podophyllum* (p. 130), *Rheum* (p.

168), *Rumex* (p. 170), *Sarracenia* (pp. 173, 177) and *Viola obliqua* (p. 186). Of these the ternately compound leaves of *Bicuculla*, which ordinarily undergo a bulbous enlargement of the basal portion, did not unfold the laminae, which remained in a condition not widely different from that shown in the bud, while the petioles did not attain a length in excess of the normal. Notwithstanding this failure to exceed the usual dimensions, the epidermal cells of the petiole were twice as long as those of normal green organs. Stomatal openings were entirely lacking and the leaves were of brief duration. *Cyclamen* offers an interesting comparison with the preceding by reason of the fact that the etiolated petioles were less than twice the length of the normal, while the epidermal cells attained a measurement of four or even five times the normal, the two examples demonstrating that the dimension of etiolated and normal organs are not correlated with the measurements of the epidermal elements. The laminae of *Cyclamen* were likewise not unfolded, but the petiole was furnished with a number of stomata apparently functional, and endured for several weeks. The petioles were apogeotropic, and a succession of these organs was produced from the corms during extended periods. The cauline leaves of *Hydrastis* developed petioles about double the length of the normal with the reniform laminae not unfolded, and the flower-bearing stems behaved in a similar manner.

A second phase of behavior of epidermal cells under etiolation is offered by *Oxalis lasiandra*, the petioles of which reach a length two to twelve times that of the normal. The increase in length is accompanied by a multiplication of the epidermal cells which are also slightly longer and narrower than in the normal. The laminar portions remained in an unfolded position with no differentiation of the tissues usually containing chlorophyl (p. 137). Only a few of the stomata were differentiated, numerous prestomatal elements with densely granular contents being discernible. The petioles were apogeotropic, falling over by their own weight, being thicker than the normal, and with the terminal portions curved upward. *Oxalis violacea* did not show such marked elongations of the petioles in darkness as the above-named species, and the tissues of the leaf reached a more advanced stage of development, with a relatively larger number of stomata, the laminae being held in an extended position approximating the normal stature. One striking feature exhibited by this plant consisted in the exaggerated development of the parenchymatous tissue in the center of the stelar tract, between and in the bundles. No definite trace was observed of a layer approximating the special pericycle found by Bonnier in the etiolated petioles of hellebore, however (see p. 28). The laminar portions of the compound leaves of *Pastinaca* failed to develop in darkness and remained in small clumps with but little differentiation of tissue. The basal portion of the leaf showed an excessive elongation and this growth was shared to some extent by the midrib, but not by the branches of the midrib. Consequently the divisions of the leaf were held farther apart than in normal leaves. The ultimate amount of growth that might be accomplished by any etiolated leaf seemed to be increased if concurrent organs arising from the same axis were removed. The duration of the etiolated leaf was comparatively brief, and the underground axis perished soon after the leaves. The cauline leaves of *Podophyllum* developed leaves in darkness with petioles much in excess of the normal (about 80 per cent.) but the laminae accomplished but a fraction of their normal superficial expansion. Stomata were not differentiated, and the leaves were of comparatively brief duration. Flower-bearing stalks bore leaves which had similar relations to darkness, but were slightly less differentiated. Etiolated leaves of *Potentilla* also had unusually elongated petioles and showed but little growth of the laminar portions. The reactions of *Rheum* and *Rumex* presented certain features in common. Both forms produced greatly elongated petioles in darkness, and made an excessive growth of the prolongation of the petiole in the lamina. The growth of the ribs of etiolated leaves of *Rheum* did not exceed the ultimate dimensions of normal leaves, but the laminae developed much more slowly and to a limited extent, so that the latter were torn and ruptured in many places by their inability to expand in the usual manner. The petiole of *Rumex* was developed to an excessive length, and the midrib also showed an abnormal growth which ruptured the feebly growing lamina. In this species the lamina was often sufficiently tenacious to set up a tension with the midrib by which it was held in a curved position. The leaves of both *Rumex* and *Rheum* were of comparatively brief duration although the former were furnished with functional stomata. A succession of etiolated organs was produced by *Rumex* during a period of several months. *Viola obliqua* developed etiolated leaves with petioles about double the length of the normal, the epidermal cells of which, had a length about four times the normal, affording an additional illustration of the fact that the dimensions of the epidermal elements are not governed by the amount of abnormal elongation of organs grown in darkness. The laminae remained smaller than the normal, and did not unfold from the rolled position of the earlier stages, and were furnished with a small number of functional stomata.

Sarracenia offers an example of a peculiar highly specialized leaf, in which the laminar tract has been converted into the walls of an ascidium. This receptacle is held in an upright position, and receives decaying organic matter, which is absorbed in greater or less quantity by the walls of the pitcher or ascidium. It is remarkable that such leaves should show a reaction in darkness generally similar to purely foliar leaves, the basal petiolar portion being excessively elongated, and the utricular structure failing to be differentiated in fully etiolated organs (see Fig. 136).

Aposeris foetida has been seen to undergo such excessive elongation of the basal portion of the sessile leaf, when grown in darkness as to become distinctly petiolate, and the midrib of the pinnate lamina also increased in length and carried the pinnae farther apart than in the normal green leaf.[179] *Beta vulgaris* bears leaves which must be classed as arising from underground stems. According to Sachs[180] these organs reach a comparatively large size with a laminar portion of a length of 11 to 12 cm., and a width of 4 to 5 cm., with the margins inrolled. The tardier growth of the laminar tissues set up a tension with the actively elongating midrib in such manner that the latter was held in a curved position.

It is to be seen therefore, that dicotyledonous leaves arising from underground organs agree in failing to produce laminae of normal structure and size, although some forms succeed in making an extended laminae, with a superficial extension approximately equal to the normal. In no instance, however, is mesophyll fully differentiated. Stomata are formed which are generally smaller than the normal organs, and not so many prestomatal elements are carried forward to the advanced stage of development as in green leaves. With but few exceptions the petioles and midribs are excessively elongated. The development of the tissues varies greatly from the normal. Parenchyma exhibits an accelerated and exaggerated growth in cortical, medullar, and fascicular tracts, which has the result in some instances of increasing the thickness of the petioles. Leaves of this group are of comparatively brief duration.

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[179] Goebel, K. Organographie der Pflanzen. Part II., p. 499. 1898.

[180] Sachs. Ueber den Einfluss des Tageslichts auf Neubildung und Entfaltung verschiedener Pflanzenorgane. Bot. Zeitung, 21; Beilage, p. 31. 1863.

Etiolation of Leaves Arising from Aërial Stems. — The remaining species included in the experimental tests embraces a number of forms of dicotyledonous and monocotyledonous plants, some of which make a distinct aërial stem, and which may bear either foliar or bract-like leaves. The following species may be included in this group: *Asparagus officinalis* (p. 73), *Aster divaricatus* (p. 78), *Cypripedium montanum* (p. 101), *Delphinium exaltatum* (p. 102), *Galium circaezans* (p. 106), *Hydrastis Canadensis* (p. 117), *Ipomœa Batatas* (p. 120), *Lysimachia terrestris* (p. 123), *Opuntia Opuntia* (p. 130), *Phaseolus*. sp. (p. 147), *Phytolacca Decandra* (p. 149), *Podophyllum peltatum* (p. 150), *Saururus cernuus* (p. 179), *Vagnera stellata* (p. 185), *Viola rostrata* (p. 187), and *Smilax Beyrichii* (p. 199). Aside from the special relations entailed by the climbing habit, the leaves of species exhibiting this capacity should also be brought under the same considerations as the above named. Special reactions were

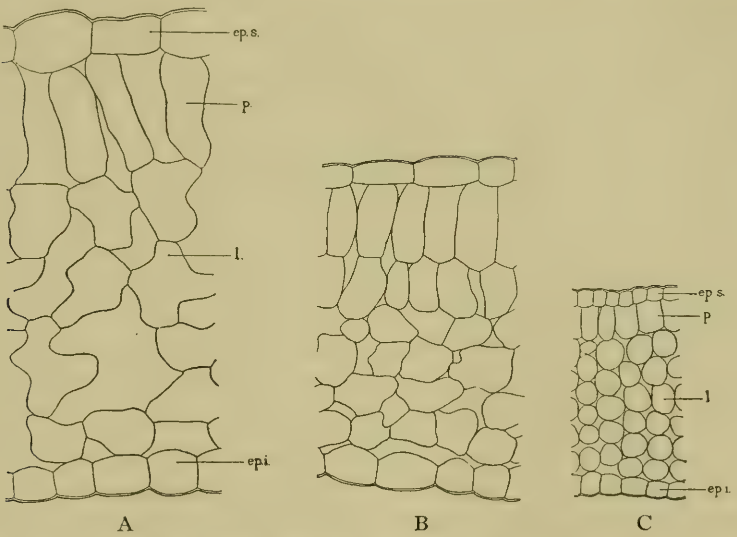

FIG. 169. Partial transverse sections of leaves of *Vicia Faba*. *A*, normal; *B*, leaf etiolated by "partial etiolation," a portion of the shoot being exposed to light; *C*, fully etiolated leaf; *ep. s.*, ventral epidermis; *p*, palisade tissue; *l*, spongy parenchyma; *ep. i.*, dorsal epidermis. After Teodoresco.

exhibited by the reduced bract-like leaves which subtend the cladodes of *Asparagus*, these organs reaching a greater expansion than on normal specimens. The attenuated fugacious ovoid leaves of *Opuntia* were larger on etiolated plants than on the normal green fronds, and were of distinctly longer duration. An interesting comparison with *Asparagus* is offered by *Smilax*. The normal leaf of the latter consists of a sheathing hypopodium, bearing a pair of tendrils on the margin about 6 to 8 mm. from the base, and passing into a distinct petiole bearing the extended lamina. Leaves developed during etiolation formed a sheathing hypopodium of a size not less than the normal, the tendrils however, being represented by two minute papillae not more than a millimeter in length. The petiolar portion was entirely lacking, and the lamina was represented by a narrow blade only a fraction of the size of the normal. The basal portions of leaves in general were found to be the least affected of any part of the foliar organs during etiolation.

The other species of this class fall into two groups, viz.; the first to include leaves arising on newly formed annual stems grown in darkness, and the second comprehending plants which form leaves from buds on perennial or hardy stems. In the etiolation of a plant of the first group it is clearly necessary that a stem should be developed from the underground member and then the leaves may arise from the internodes, making necessary a much greater morphogenic and physiologic effort than when plants of the second group are awakened in darkness. In the latter instance the buds, which may be more or less numerous, begin to elongate and a leaf may arise from the first internode which on stems of the first kind ordinarily may bear only a bract or some form of a reduced foliar organ.

Leaves of *Aristolochia*, and *Aster* developed excessively elongated petioles in darkness, which with the undeveloped laminae were held in various abnormal attitudes. A tendency to assume an apogeotropic position, or one more or less appressed to the stem, by the petioles, was noticed in the species included in this group, although *Apios* among the climbers formed petioles shorter than the normal. The laminae of *Aster* did not unfold, and remained in a very primitive condition, the leaves having a very brief duration in darkness. Etiolated leaves of *Cypripedium* were twice the length of normal organs, but were of decreased width, in contrast with the leaves of *Vagnera* which were both shorter and narrower than the normal. The pinnatifid leaves of *Brassica* underwent an excessive elongation of the basal portion, thus producing a long petiole in etiolated organs, and was held in a position more nearly upright than in normally cultivated plants. The entire etiolated laminae was extended, but only a small proportion of the stomata attained full differentiation. Etiolated leaves of *Delphinium* had petioles two to five times the normal length, and the laminae remained in closely rolled clumps, with but little capacity for transpiration. In this, as in the species described above, the etiolated petioles were held in a position more nearly upright than in the normal (see also *Gasteria*, p. 109). *Galium* offered a curious reversal of the action shown by *Aposeris* and other leaves in which exaggerated growth of the basal portion of the leaves ensues in darkness, for the narrowing of the basal portion of the leaf to a petiolar structure was entirely lacking in etiolated plants of the former. The leaves arising on aërial stems of *Hydrastis* subtending the peduncles did not make any increased growth of the basal portion and reached but a fraction of their normal extension. Etiolated leaves of *Ipomœa* developed leaves of ordinary proportion of lamina and petiole, both being smaller and shorter than in the normal, and were held in an erect position. The sessile leaves of *Lysimachia* did not show any attenuation of the basal portion when etiolated, and were much smaller in all dimensions than normal organs, also being held in an appressed position against the stem. Leaves borne on branches of stems of *Phaseolus* which were thrust into dark chambers in "partial etiolations" after the manner used by so many investigators had extended and unfolded laminae, which were held in more or less nearly normal positions, while those of fully etiolated seedlings had petioles of a length much less than the normal, being simple, and were held in an erect position, or appressed against the stem. Etiolated leaves of *Phytolacca* were smaller both as to petiole and lamina than the normal, being only a fraction of the size of normal organs. The two leaves borne on the flowering stems of *Podophyllum* showed diverse reactions. Ordinarily these organs are fairly equal in size, but in etiolated plants, the petioles might be elongated beyond normal dimensions, or might be nearly sessile, owing to the non-development of the petiole. Moreover, in all instances the pair of leaves failed to make an equal growth (see Fig. 111), the laminae reached an extension much less than that of the normal, being held in various distorted positions. Etioled leaves of *Saururus* developed only short petioles, the clasping bases of which failed to keep pace with the thickening of the stem and hence were soon cast off. The laminae remained closely rolled and in a very primitive condition. The petioles were held in a position variously appressed and the laminae were distorted and the edges of the same were inrolled. Etiolated leaves of *Viola rostrata* consisted of an excessively elongated petiole which assumed an erect, or at times a horizontal position in older organs, and a lamina which did not unfold and which was held in various positions by the curvature of the petiole below the lamina.

Only a comparatively small number of plants with perennial aërial stems were cultivated in the dark room, and most of these have already been discussed in various other groups, but it will be profitable to consider the action of the leaves with reference to the character of the stems from which the etiolated leaves arise. The species included are as follows: *Acer rubrum* (p. 188), *Baccharis halimifolia* (p. 80), *Cornus alternifolia* (p. 97), *Fagus Americana* (pp. 105, 194), *Populus Simonii* (p. 154) and *Quercus* (p. 166).

Etiolated leaves of *Acer* consisted of a petiole much shorter than the normal and a lamina which was fully extended with an outline approximating the normal form, but much smaller in superficial area. Functional stomata were present and the leaves had a duration of about twenty days. The suggestion arose during the course of the experiments that the awakening of the leaves of this plant was stimulated by illumination. The position of etiolated leaves was determined by their evident apogeotropism. Etiolated leaves of *Baccharis* did not exhibit any tendency to an excessive elongation of the basal portion, not attaining normal dimensions and were of brief duration. Etiolated leaves of *Cornus* were much smaller than the normal, preserving the ordinary relations of lamina and petiole, and were held in various positions. Etiolated leaves of *Populus* offered similar reactions, the proportions of the petiole and the lamina being about the same as in the normal and both being much smaller than in normal specimens. Here, as in *Apios*, the stipules were nearly normal size and stature, being but little reduced. The leaves of *Quercus* assumed positions which in some instances were fairly normal and the laminae were relatively more developed than the petiole, the entire leaf being but a fraction of the size of the green organ. The fibrovascular bundles were more clearly separated in etiolated leaves, but no distinct individual pericycle could be made out as in hellebore (p. 28). *Fagus* developed leaves in darkness which were of briefer duration than normal organs, and in which the petioles and laminae were of the ordinary proportions but much smaller than in the normal. The laminae were extended and were held in positions approximately normal. The awakening of the buds of this plant have been found by Jost and myself to be influenced in a very important manner by illumination.

A comparison of the data obtained by the etiolation of leaves borne on aërial stems leads to the following general considerations. Leaves of woody, hardy or perennial stems did not attain normal dimensions in any instance, although wholly unfolded and extended in a normal manner in some species. In no instance did the petioles undergo an excessive elongation. On the other hand, leaves arising from tender herbaceous stems, which were produced from underground members in darkness generally showed an exaggerated elongation of the petiole, if a distinct petiole were present, and in a few instances, a sessile leaf produced a petiolar stalk by the attenuation of the basal portion. *Saururus*, *Smilax* and *Phytolacca* are examples of forms in which the petioles behaved much like those of woody plants in not making an excessive growth, while *Galium* and *Lysimachia* are to be cited as furnishing sessile leaves which failed to develop a distinct stalk in darkness. *Vagnera* produced etiolated leaves shorter and narrower than the normal, in contrast to the other monocotyledonous species, including *Coix*, *Zea* and *Cypripedium*, in which the laminar portions of the leaves were elongated to dimensions at least as great as the normal, and in excess of the normal in some instances. An inspection of the data at hand does not afford any means by which safe generalizations may be made as to the behavior of all leaves in darkness. The general habit of the plant, the availability of the food-reserve, the morphological character of the axis, and of the leaves, may play a part in the determination of the reactions, but so far the exact influence of each of these factors has eluded analysis.

It may be said however that the growth and development of foliar organs is similar to that of stems in the fact that the multiplication and growth of the parenchymatous elements, particularly in the stelar tracts is greater than in the normal, and is not accompanied by the customary morphological differentiation, the failure to achieve normal development being most marked in the tissues ordinarily carrying on the photosynthetic functions. The facts secured in the investigations furthermore disturb many currently accepted conclusions. Among these is "that growth in breadth is in all cases hindered or prevented by darkness,"[181] since it has been found that the leaves of many species, principally monocotyledonous forms with parallel veins, do attain a width equal to the normal, of which *Hyacinthus*, *Narcissus* and *Tipularia* are examples. Sachs and other workers have found a width less than the normal in leaves of *Narcissus* and *Hyacinthus*, but in the etiolative experiments described in this volume the leaves were flattened mechanically until the laminae were in a plane when the measurements taken gave the above results. It seems justifiable to conclude that the amount of growth and development achieved by an etiolated leaf may be dependent to some degree upon the degree of development which these organs have made during the formation of the bud in which they are enclosed, a consideration to which Sachs has previously called attention. In this instance the full effect of etiolation might be obtained only by the culture of the plant for a second season in continuous and complete darkness. If this condition is taken into account it is doubtful if any plant develops leaves of either normal length or width in darkness. So far as the records are available the hypopodial region of the leaf is least affected by etiolation. The bract-like leaves of *Asparagus*, the small leaves of *Bowica*, and the leaf-bases of *AEsculus* attained a size in darkness not less than that in light. Then the stipules of *Apios* and *Populus* did not suffer any marked reduction as a result of etiolation. The broad leaf-bases of *Smilax* were similarly resistant to the reducing effects of etiolation, although the tendrils arising from these bases were markedly affected. So far as the activity of the cells is concerned the processes of division and multiplication as well as actual enlargement of the elements in various forms has been found to go far beyond the normal in many instances, and it is evident that no part of the behavior of the leaf may be attributed to the direct action of illumination upon the cells, but that organs react as a unit to whatever forces constitute the dominant factors in producing the abnormal forms characteristic of etiolations.

Etiolation of Flowers and Inflorescences. — The greater number of species examined failed to produce flowers or special reproductive bodies of any kind, either sexual or asexual, in darkness. A consideration of the facts described however, should take into account that in the processes entailed in the formation of flowers, seeds and spores, temperatures and nutrition must be adjusted even more delicately than for the vegetative processes, so that many of the plants examined might have developed flowers or sporophylls at higher or lower temperatures approximating their specific maxima. The only species which produced flowers which in a measure were approximately similar to the normal were the following, viz.: *Amaryllis* (p. 40), *Amorphophallus* (p. 40), *Arisaema* (pp. 48 and 50), *Hypopitys* (p. 119), *Hydrastis* (p. 117), *Podophyllum* (p. 150) and *Trillium* (pp. 181 and 182), in which the flowers including the pistils and stamens were laid in their definitive form during the previous vegetative season, and their growth consisted chiefly in an enlargement of the tissues and parts already formed. Thus it is notable that *Arisaema* did not produce flowers in the second season of its etiolation although furnished with sufficient reserve to enable it to send up leaves for two seasons following. An interesting reaction by *Arisaema* was seen in the formation of a second scape and flower on an etiolated plant brought into light (p. 60.) In no instance, except in *Hypopitys*, were seeds formed in the etiolated cultures. Pollination was effected mechanically, but no demonstration could be made as to whether actual fertilization ensued or not. Likewise no mature and functional spores were produced by any of the ferns which were cultivated in the dark chamber. So far as could be learned the flowers of *Hypopitys* carried on their activity in the usual manner, it being the only species which produced seeds when grown in complete darkness, but the difficulty of securing germinations made it impossible to apply the final test to the perfectness of the seeds. The inflorescences of *Aplectrum*, *Narcissus*, *Tritelia* (*Milla*), and others did not emerge from the sheathing scales. The peduncles and scapes were generally elongated beyond the normal, although this was not the case in *Trillium* and *Hydrastis*. The members of the floral envelope were generally smaller than in the normal, the corolla being wholly undeveloped in a test made with *Salvia* in which an entire plant was placed in a dark chamber after the flowering branch had been formed. The non-green colors were developed in a manner fairly similar to the normal, but the absence of chlorophyl and the altered opacity of the tissues made this difficult to determine with accuracy, and the general color scheme was materially changed.

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[181] Vines, S. H. Physiology of Plants, p. 381. 1886.

The alterations of flowers in response to darkness have been the subject of many investigations, but the results recorded by the various workers who have interested themselves in this subject are somewhat difficult of comparison. The chief difficulty in the interpretation of the facts at hand consists in the fact that in some instances plants were allowed to grow until the inflorescences and the flowers were more or less completely formed and then the entire plant was placed in a dark chamber, which might be opened and examined in the full blaze of daylight at frequent intervals. In other instances, plants were taken at an advanced stage as above, and the inflorescence, or the branch bearing it were thrust into a dark chamber more or less imperfectly sealed against light, thus making a "partial etiolation." In still other researches the plants were taken at an earlier stage and the inflorescence allowed to carry on its full development in darkness, but with the remainder of the plant exposed to light. All of these methods entailed inexact observations in which no control of the temperature and humidity of the air around the flowers was kept. Attention is to be called to the fact that the stimulation by which darkened buds may be awakened by illumination of others on the same shoot doubtless has a similar effect on flowers and that all "partial etiolations" must be disregarded in the effort to discover the effect of darkness upon flower-formation. Furthermore, only evidence may be admitted which has been obtained from plants in which the entire development of the flower proceeds during the vegetative season in which it opens or blooms. Under these conditions the conclusion is inevitable that flowers are not produced in darkness, except in *Hypopitys*, and it is probable that a similar phenomenon is exhibited by *Ephiphegus*, a chlorophylless parasite.[182] This is correspondent to the results of etiolation of *Coprinus* and other fungi in which spores are not perfected in darkness.

Senebier[183] relates that Mees observed that beets flowered in cellars, and he himself describes his own observations in which tulips and crocuses were seen to produce flowers in "partial etiolations." The inflorescences of *Narcissus* did not emerge from the etiolated sheathing bracts and peduncles were seen to undergo excessive elongation in darkness. Tulips were found to offer as well-marked color of flowers in etiolated plants as in those cultivated in light. Sachs removed the flower buds and fruits from a well-grown specimen of *Nicotiana rustica* and placed it in complete darkness, with the result that two inflorescences were developed on etiolated branches about 11 days later. The earlier flowers developed in these inflorescences were yellow, but otherwise of normal appearance. Self-fertilization ensued and capsules of a size above the average were formed, the seeds taken from which germinated when placed in the soil. He states, however, that the calices of the lower flowers of the etiolated inflorescences were green from the influence of illumination received before the plant was placed in the dark chamber; hence the flowers did not undergo their entire development in darkness. Scapes of *Hyacinthus orientalis*, *Tulipa Gesneriana* and *Iris pumila* were seen to attain a length of three times the normal on bulbs sprouted in darkness. In *Crocus vernus*, on the other hand, the scape remained of a normal length and an excessive elongation ensued in the basal portion of the perigone tube. Sachs cites *Tulipa*, *Iris*, *Hyacinthus* and *Crocus* as examples of plants in which the flowers are formed in buds deep in the ground, consequently in darkness, and that flowers of this class can consequently carry on complete development in darkness without ever being exposed to the full influence of sunlight. In this however, a disregard is shown for many facts bearing upon the case. In the first place it is by no means conclusive that the tubers of these plants are in complete darkness when in place in the soil under natural conditions. Even if completely excluded from the effects of direct illumination, it is to be seen that the formation of the flowers in the season previous to the one in which they open, takes place while some of the organs, such as the leaves, are exposed to light, and that the full stimulating effect of this partial illumination doubtless exerts a marked effect upon the young flowers. It was shown in my own experiments that *Arisaema* and similar forms did not develop flowers when the plant was confined in darkness for successive seasons, although ample food-material was present. *Brassica*, *Tropaeolum*, *Papaver*, *Cucurbita* and others, are given by Sachs as constituting a class of plants in which the flowers will not open if deprived of illumination at a time beginning with the earlier stages of the flower buds. The normal blooming of such flowers when confined in darkness after an advanced stage of development had been reached is clearly not an etiolative reaction in any sense of the word. In another series of observations, by means of partial etiolations, the apical portions of shoots were thrust into dark chambers, and in some instances new flower buds of *Cucurbita* and *Petunia* arose on branches from which light had been excluded in this manner, which came to a development more or less nearly approximating the normal, except in the matter of color. As a result of these facts Sachs concluded that the development of flowers was dependent upon peculiar substances resulting from the action of light on chlorophyl-bearing tissues, and that the failure of etiolated plants to produce flowers was due to the lack of such material. In partial etiolations an opportunity was afforded for the production of this specific material in the illuminated leaves, which then might be easily conducted to the flowers much in the same manner as under normal conditions. An etiolated flower grown under the above conditions was fertilized from pollen grown in the open, with the result that a ripe fruit was finally produced in the dark chamber that weighed 3 kilos. (Given as 4 kilos in Sachs' Phys., p. 533. 1887.) Seed was also produced on a number of other species by similar "partial etiolations." In a later investigation Sachs [184] believed to have demonstrated that the ultra-violet rays furnish the energy by which a specific anthogenic substance is formed and without which these organs are not produced.[185]

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[182] Leavitt, R. G. Subterranean plants of Epiphegus. Bot. Gazette, 33: 376. 1902.

[183] Senebier, J. Observations sur les fleurs du quelques plantes élevées dans l'obscuritié. Mem. Physio-chimiques, 2: 99. 1782.

C. DeCandolle repeated Sachs' experiments in 1892, cultivating a number of plants in light which in one series had passed through a layer of water, and in another through a layer of sulphate of quinine or aesculin by which the plants were screened from the action of the ultra-violet rays in the latter. "He found no flowers in two plants after cultivation behind a screen of solution of sulphate of quinine for seventy-one days; thirty-three flower buds in two plants grown behind an equally thick screen of water; behind a screen of aesculin flowers were formed in *Lobelia erinus*, but in smaller numbers than behind water."[186] The results in question are not conclusive that the ultra-violet rays take a part in the construction of any specific material. All of the phenomena in question might well be ascribed to the stimulative action of light as suggested by DeCandolle. So far as the relation of the screened and control plants are concerned experiments of this character must be made with the greatest care, since a small difference in the intensity of illumination might inhibit or induce flower-formation irrespective of the actual composition of the spectrum. Here as in other operations of the plant, the formation of flowers or reproductive bodies requires a certain optimum intensity of illumination and any variation beyond certain limits will have the consequence that such activity will not ensue, a conclusion well justified by the careful researches of Vöchting,[187] who found that light sufficient for the normal vegetative activity of a plant did not necessarily coincide with the amount necessary for the formation of flowers. A repetition of Sachs' "partial etiolations" with *Cucurbita* by Amelung, in 1893, gave results in accordance with those previously obtained by the former in so far as the production of flowers and fruits was concerned. Flowers of fairly normal aspect developed from young buds placed in darkness, but the flowers which arose entirely in darkness attained a lesser size as the distance from the illumination portion of the stem increased. The earliest functional atrophies were found in pollen, the etiolated cells of which were incapable of carrying out the fertilization processes, the stamens showing more marked effects of the confinement in darkness than the pistils. The size of etiolated pollen grains varied from a diameter of 22 to 29, while that of normal grains ranged between 26 and 27. The extine, intine and cytoplasm gave a fairly normal appearance when treated with Grenacher's borax-carmine, but the two nuclei had undergone such degeneration as to have disappeared, or perhaps but one remained. The gametophyte hence appears to sustain general relations to light similar to that of the spores of ferns.[188]

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[184] Sachs. Ueber den Einfluss des Tageslichts auf Neubildung und Entfaltung verschiedener Pflanzenorgane. Bot. Zeitung, **21**: Beilage, p. 31, 1863, and Wirkung des Lichts auf die Blüthenbildung unter Vermittlung der Laubblätter. Bot. Zeitung, **23**: 1865.

[185] Sachs. Ueber die Wirkung der ultravioletten Strahlen auf die Blüthenbildung. Arb. a. d. bot. Inst. i. Wurzburg, **3**: 372. 1887.

[186] Goebel. Organography of Plants. Part I. p. 244. 1900.

The researches of Askenasy,[189] which were made by means of various imperfect and partial etiolations, led him to conclude that the non-development of flowers in darkness was due to the lack of a proper amount of food-material in the shoot, rather than to the abscence of any specific substance. Vöchting[190] found that flower-buds failed to open, or make full development in *Dolichospermum Halicacabum*, *Tropaeolum Lobbianum* and *Mimulus Tillingii*, and did not open when grown in chambers, the atmosphere of which was entirely free from carbon dioxide. That the failure to carry out flower-formation in the usual manner was due to lack of suitable nutrition is not entirely clear in the light of the recent researches of Brown and Escombe[191] upon the influence of atmospheres containing more than the normal proportion of carbon dioxide. The atmosphere usually contains about 28 parts of carbon dioxide in 100,000, and when plants were confined in ventilated chambers through which air containing 114 parts of carbon dioxide in 100,000 "inflorescence was almost totally inhibited." "With the exception of one or two sickly-looking flowers on the begonias, not a single flower-bud opened on any of the plants of this set." "The plants of *Impatiens*, *Kalanchoe*, and of the darker leaved fuchsias did not even produce flower-buds, whilst in *Nicotiana*, cucurbitas and lighter leaved fuchsias, the smaller flower-buds which commenced to form were completely shed long before the time of opening." The rate of absorption and use of carbon dioxide by the plant was found to increase with the proportion of this substance in the atmosphere up to certain limits, but the products of the photosynthetic activity of plants grown in such atmospheres evidently could not be handled by the conducting mechanism and general metabolic complex of the plant, for the dry weight of specimens grown in atmospheres richer than the normal in carbon dioxide was less than the average of plants grown in ordinary air. Stems grown under experimental conditions with increased proportions of carbon dioxide were composed of shorter internodes, but these members were increased in number so that the plants reached average height, although deviating from the normal stature by the development of a greater number of axillary buds by which the shoots were made more dense in their general aspect. Nothing in the above experimental observations could be found to suggest a direct poisonous action of carbon dioxide on the plant.

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[187] Vöchting. Ueber den Einfluss des Lichtes auf die Gestaltung und Anlage der Blüthen. Jahrb. f. wiss. Bot. 25 : 149. 1893.

[188] Amelung, E. Ueber Etiolement. Flora, 78 : 204. 1894.

[189] Askenasy, E. Ueber der Einfluss des Lichtes auf die Farbe der Blüthen. Bot. Zeitung, 34 : 1, 27. 1876.

The recent results by Chapin become of direct interest in this connection since he found that the rate of growth of higher plants during short periods of exposure was greatest in atmospheres that contained 1,000 to 2,000 parts of carbon dioxide in 100,000 and that a poisonous action was exerted by an amount of carbon dioxide in the atmosphere equal to 20,000 parts in 100,000.

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[190] Vöchting, H. Ueber die Abhängigkeit des Laubblattes von seiner Assimilationsthätigkeit. Bot. Zeitung, 49: 113, 129. 1891.

[191] Brown and Escombe. The influence of varying amounts of carbon dioxide in the air on the photosynthetic processes of leaves and on the mode of growth of plants. Phil. Trans. Roy. Soc. 193: 278. 1900. Abstract in Nature, 66: 621. 1902.

Nothing in the last-named investigation appears to disturb the conclusion that the plant is in a tonic condition for the production of flowers only when the carbon doxide of the atmosphere exerts its customary pressure, and any deviation from this standard is followed by an inactivity of the flower buds.[192]

Bonnier found that the effect of continuous electric illumination upon the flowers of such plants as the tulip and hyacinth was to deepen the colors and to produce closer and denser inflorescences. Bailey saw that the influence of electric illumination used to supplement daylight was to bring the opening of the flowers a week earlier than in the normal, in some species, but only about four sevenths of the average number of seeds was produced. In general the colors of flowers were intensified in the earlier stages of blooming, and sometimes an increase in the size and number of flowers could be seen in such forms as *Petunia*. Rane observed that the formation of flowers occurred a few days earlier in plants that had been given an artificial supplementary illumination in addition to normal daylight (see references on page 210), and Corbett found that some plants of spinach under the influence of additional artificial illumination produced flower stalks, while normally grown specimens failed to show any formations of this character. The most recent formal investigation of the relation of the flower to light has been made by Beulaygue,[193] but the principal method used in his work consisted of partial etiolations in which flowering branches and inflorescences were thrust into small dark chambers after the manner used by Sachs and others, and hence his results have but a restricted value. Under the conditions mentioned there was shown a lack of formation of flowers, a number below the average, or a tardier appearance of the flowers that were formed. Flowers etiolated in the manner indicated were smaller than the normal, decoloration was more or less complete, and the pedicel underwent an excessive elongation while attaining a diameter less than the normal. These external alterations were accompanied by modifications of the structure of the tissues of the various parts of the flower. Parenchymatous cells were larger and showed a multiplication of their number in some instances. Both pollen grains and ovules were smaller than in the normally grown flower.

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[192] Chapin, P. Einfluss der Kohlensäure auf das Wachstum. Flora, 91 : 348–379. 1902.

[193] Beulaygue, L. Recherches physiologiques sur le dévelloppement de la fleur. Montpelier. 1901.

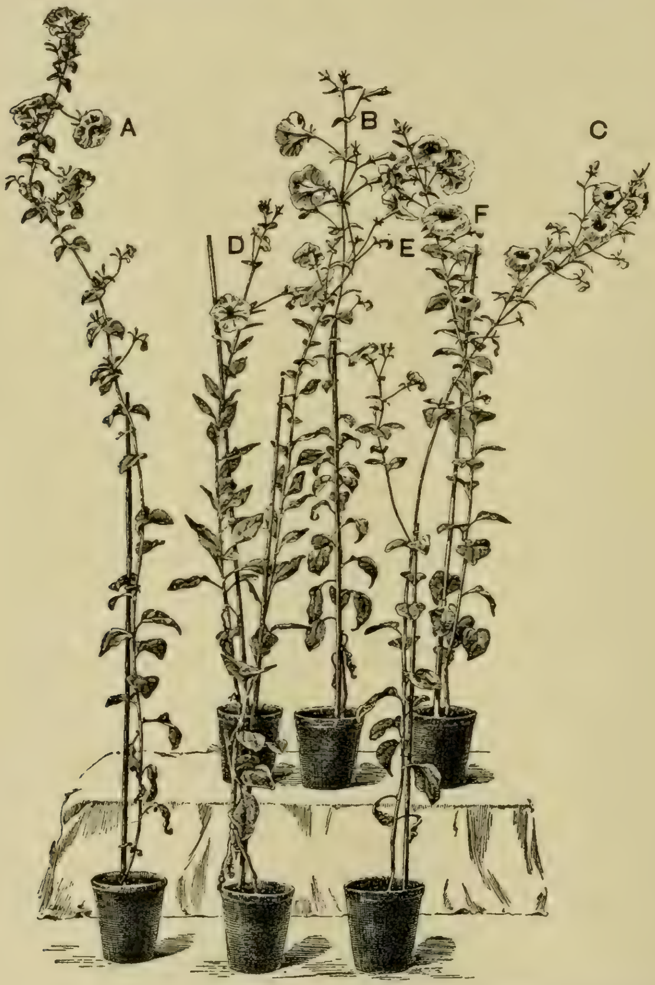

FIG. 170. *Petunia.* *A*, *B* and *C* grown under conditions in which daylight was supplemented by electric illumination. *D*, *E* and *F*, normal. After Bailey.

It appears therefore that no autotropic chlorophyllose species develops flowers unless the buds are subjected to the action of light during some part of the period of development, or that some portion of the shoot in close organic connection with the inflorescence should be subjected to the action of the rays during some portion of the period. *Hypopitys* appears to be indifferent to the action of light and makes both flowers and seeds in darkness. Seed formation is accomplished in darkness if the inflorescence is exposed to illumination during a portion of the earlier stages of development of the flower, and also in the flowers formed earliest in " partial etiolations," but not in later ones. In the last-named instance however, the introduction of pollen taken from illuminated specimens seems to be necessary. The pistils show least atrophy during such partial etiolations, as the stamens are reduced earlier. It would be difficult to maintain that the non-formation of flowers in darkness is due to the lack of some specific formative substance, as suggested by Sachs. The development of the flower and the perfection of the embryo-sac and stamens entail important morphological differentiations, which it has been shown, have failed to occur in the vegetative portion of the plant. It seems much more probable that the highly specialized groups of cells ordinarily differentiated in the development of the pistil, stamens, and the embryo, and in the integration of the seed should fail to carry out their normal procedure from the same causes as those affecting stems or other members of the body. The failure to effect the usual differentiations brings as an enforced consequence the lack of completion of the gametophytes, and of the complicated structural changes following fertilization and terminating in the construction of the complex seeds and fruits. From this point of view, the incomplete pollen cells found in all etiolated plants ordinarily green is not due to the direct lack of the action of light upon the stamens but to an incomplete state of morphological development which has not brought these bodies up to their functional maturity.

It seems justifiable to take the position that flower formation is accomplished only when any given species is exposed to an illumination approximating a specific optimum, and that any deviation from this is liable to inhibit the process entirely, or perhaps alter the method of procedure in such manner that cleistogamic instead of chasmogamic flowers may be produced. The procedure in question would imply but a small departure from the customary activity. If the species which produce subterranean flowers are now taken into consideration it may be seen that a second adaptational type is reached by which flowers are constructed without the aid of direct illumination, thus making untenable the theory that the action of light in producing specific formative substances is necessary for the construction of flowers, the perfection of the gametophytes, and their functional activity in setting up the changes antecedent to the integration of the seed. Stated in another form the relation of the flower to illumination is seen to be purely adaptational and whatever action the rays may exert upon it must be classed as stimulative in their actual effects. This will be still more vividly apparent when the matter of development of sporophores, sporophylls, sporangia and spores is considered; since the most diverse reactions are exhibited by the ferns and fungi when deprived of illumination.

Effect of Etiolation upon Spores and Sporangia of Ferns. — Sporangia were entirely lacking from etiolated leaves of *Asplenium platyneuron* (p. 75), and the sporophylls of *Botrychium* (p. 81) were atrophied in a very early stage of its development. No sporangia could be found in *Filix fragilis* (p. 106), and the sporophylls of *Onoclea sensibilis* and *Osmunda cinnamomea* were not developed in etiolated cultures. No differentiation of the sporogenous tissues ensued in *Polystichum acrostichoides*, *Pteris longifolia*, or *Woodwardia radicans*. The appearance of the sporangia in all of the species mentioned usually occurs at the summit of the morphological development of the sporophyls, and the notably incomplete stage of differentiation of the tissues reached by all of the species in darkness renders the formation of sporangia or the completion of spores impossible.

Goebel suggested that a relation between illumination and the formation of sporangia in ferns similar to that of the higher plants to light some time since, but chiefly with reference to a possibility of the conversion of sporophyllary to foliar leaves and vice versa. (Flora, 80: 116. 1895.) In many of the species of ferns examined by etiolated methods with results as enumerated above, ample reserve food was to be found in the rhizomes and all ferns agree in the production of chlorophyl in darkness. Here, as in the higher plants, the lack of the necessary condition of a certain completeness of morphological differentiation of the sporophyll preliminary to the development of sporangia rendered the formation of spores impossible. The differentiation of the tissues in question is, as in the higher plants, dependent upon the stimulating action of light.

Sporophylls of *Equisetum* attained a development fairly comparable to the normal but the spores were not completed. Exact evidence as to the condition of these structures before etiolation began was not obtained.

Relation of Sporophores and Sporangia of Fungi to Light and Darkness.—When the facts obtained by the observations of the behavior of fungi in light and darkness are brought under consideration it is to be seen that these plants present the greatest diversity of reaction. Some species do not make any alteration in form in response to illumination and darkness, while others carry on the formation of sporophores in light only, or in darkness only. The example of *Coprinus* may be taken to illustrate one phase of this action. This plant develops a length much greater than the normal in darkness, with the sporangia remaining in a rudimentary or incomplete stage. After growth has proceeded in this manner for some time the illumination of the body is followed by the production of sporangia in a manner demonstrating most conclusively that the action in question is due to a purely stimulative action of light, since the rays do not participate in any synthesis of material.

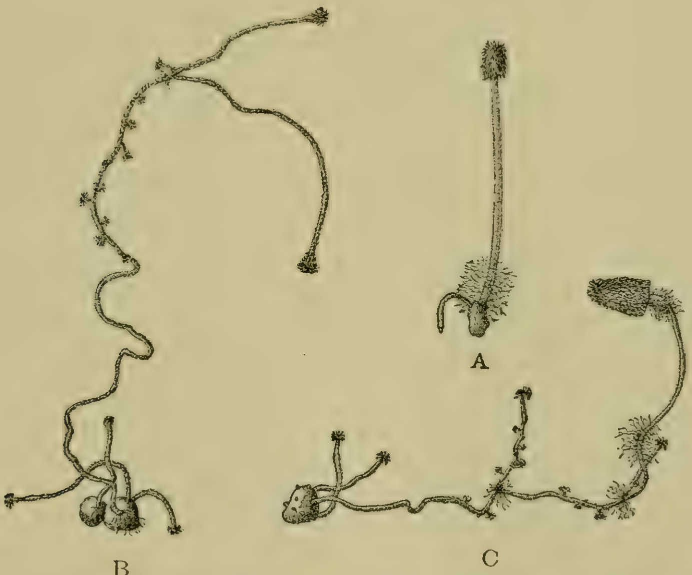

FIG. 171. *Coprinus stercoriarius.* *A*, normal; *B*, grown in darkness; *C*, etiolated culture which has been exposed to subsequent illumination. After Brefeld.

The recent results obtained by Potts[191] show that the growth of the sporophores of *Dictyostelium* is retarded when cultivated in the open air, but when confined within a damp chamber a growth above the average normal is made, showing that light does not retard growth in this species, and that the lessened growth in the open air under the action of light may be ascribed to transpiration, although interpreted in another manner by Potter.

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[191] Potts, G. Zur Physiologie des *Dictyostelium mucoroides.* Flora, 91: 281–347. 1902.

THEORIES AS TO THE NATURE OF ETIOLATION.[194]

Various explanations have been advanced to account for the abnormal form, stature, color, structure, growth and development of plants in darkness, beginning with the time of Hales (1727), and the theories formulated constitute a most interesting index of the state of knowledge of the physiology and morphology of plants during the last two centuries. Hales ascribed the greater length of the attenuated etiolated stems which came under his observation to the increased ductility of the tissues, a view which A. P. DeCandolle, shared a century later (1832). Very naturally the earlier investigators laid the greatest stress upon the more apparent physical features in which alterations were to be easily observed, and consequently the matter of color came in for an undue share of attention, while the lack of information as to the character of the photosynthetic functions, and of the general morphology of the plant made it impossible that the functional and anatomical alterations due to the absence of the morphogenetic and other influences of light should be appreciated. To Senebier perhaps (1800) may be ascribed the first serious attempt at an explanation of the abnormal manifestations shown by etiolated plants.[195] He assumed that the primitive or fundamental color of plants was yellow, and that etiolation inhibited the processes of oxygen-separation and carbon-fixation that were necessary for the construction of the various colors. The lesser dry weight of etiolated plants when compared with those grown in light was assigned to the lack of formation of carbon compounds, and to an increased retention of water. The last statement is, of course, fairly correct so far as our present knowledge of the subject bears upon the matter, but the other portions of his explanation do not need further attention. A few years later (1811), Ellis[196] made an examination of the facts presented by Senebier, and without the addition of any further observations questioned the conclusions of the latter as to the alterations in color and the lack of chlorophyl in plants grown in darkness, and advanced the supposition that the abnormally large amount of carbon dioxide in etiolated leaves would destroy the green color and, "Hence, therefore, the etiolated state of plants depends on a deficiency of alkaline, or a superabundance of acid matter, by which the usual operation of the alkali is reduced or counteracted ; but the sun's rays, by withdrawing and decomposing this excess of acid, enables the alkali to resume its former action, and thereby restore the green colour of the leaf." No actual contribution to the subject was made until the time of Sachs (1859–1892), and Kraus (1869). The latter attributed the excessive elongation of stems to the abnormally high tensions of the parenchymatous tissues, the cells of which not only increased in length far beyond the normal limits, but also showed an increase in number, thus stretching the ductile stems beyond the normal limits. The failure of the leaves to attain normal dimensions was accounted for by the supposition that these organs were capable of growth only by means of material constructed locally by their own activity and hence, were incapable of development in darkness (see pp. 11 and 12). It is to be said that the excessive elongation of stems in darkness is accompanied by either an exaggerated growth, or multiplication of the cells of parenchymatous tissues, or by both, and that the excessive increase in length or thickness of stems in darkness is due in part to the action of these tissues, although other tracts are active as well. The alterations in form are, as a matter of fact, due to the correlated action of the entire body of the shoot and may not be ascribed to any one set of cells. It has been demonstrated by Jost, Sachs and myself that leaves may carry on development in such manner as to be able to attain a stature approximately normal as to extension and size when relieved of the competition of concurrent organs and furnished with a supply of food-material, although in such instances the customary morphological differentiations do not ensue.

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[194] Presented before the New York Weekly Botanical Convention, Museum of the New York Botanical Garden, November 5, 1902.

[195] Senebier. Hypothèse pour expliquer l'etiolement. Physiol. végétale. **4**: 295–308. 1800.

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[196] Ellis, D. Farther inquiries into the changes induced in atmospheric air by the germination of seeds, the vegetation of plants and the respiration of animals. p. 132. 1811. Edinburgh.

Sachs' researches were so extensive and included so many of the phases of the subject that it will be profitable to take up at this point only those which attempted an explanation of the nature, or the cause of the etiolative phenomena, and as his point of view naturally changed considerably in the thirty years in which he had this subject under consideration it will be necessary to touch only upon the conclusions he was disposed to consider as final (pp. 7–11). The abnormal form of etiolated leaves was regarded as due to pathological conditions, as the result of some investigations carried on by Prantl (p. 13, 1873) in Sachs' laboratory, and the reduced size of many plants including seedlings grown in darkness was attributed directly to lack of nutritive material, although he distinctly disclaimed approval of Kraus' self-nutrition theory as he found that leaves on portions of shoots confined in dark chambers in partial etiolations attained considerable size. The unusual elongation of stems was determined by him to be due to the increased size of the cells rather than to a multiplication of these elements, and to take place in the absence of the paratonic or retarding influence, which he supposed was exerted on growth by light. An important feature of Sachs' explanation of the phenomena of etiolation was that specific formative material was necessary for the construction of the various organs, particularly flowers. Flowers could be developed only when the buds were laid down and supplied with anthogenic material which was a product of leaves in sunlight, and might not be replaced with building material from storage organs. He anticipated in a suggestive way the "adaptive theory" of etiolation when he described the stems of climbing plants as "naturally etiolated," and thus incapable of any further effort to reach sunlight by excessive elongation. Lastly he believed to have demonstrated that the action of the ultra-violet rays of the spectrum were necessary for the formation of the special anthogenic or flower-forming substances, and that these rays exerted an important influence upon the growth and development of plants. Of these several contentions it is to be said that the extended endurance of etiolated leaves, and of other organs to confinement in darkness, and the fact that fully etiolated members are capable of taking up normal development when brought into normal illumination lead to the conclusion that etiolation is not necessarily a pathological condition, a statement corroborated by the condition of the protoplasts of the organs in question. As pointed out previously, both increase in size and multiplication of elements ensues in etiolated organs, and his generalization upon this subject becomes worthless in the light of extended observations. The stems of climbing plants have been shown by myself to be not "naturally etiolated" but to owe their behavior in darkness to other and more direct physiological causes. The failure of the greater number of the conclusions of Sachs to stand the test of modern observations must be taken to rest upon the fact that his experimental evidence was obtained chiefly by "partial etiolations" and to the growth of plants under conditions in which the action of light was imperfectly excluded. The assertions of Sachs as to the necessity for special formative materials, and the action of the ultra-violet rays as to the retarding influence of light upon growth will be taken up in the following pages.

Batalin (1869, 1871) set himself against the "self-nutrition" theory advanced by Kraus in explanation of the non-development of leaves and other etiolated organs, and attributed their atrophy to the incapacity of the plant to carry on cell-division in the shoot in the absence of light, the rays supposedly exerting a direct influence upon the tissues (pp. 11, 12) in normal shoots. Rauwenhoff (1878) also held that the abnormal condition of leaves in darkness was partly pathological, and that the characteristic positions of etiolated organs were due to geotropic reactions unhindered by phototropism, and modified to some extent by the unusual conditions of the tissues. The interpretation of etiolation as a direct adaptation, and the assumption that the attenuation, or elongation of axial organs as a means of lifting chlorophyl-bearing surfaces past a theoretical obstruction, seems to have originated with Boehm in 1886, although not elaborated until taken up by Godlewsky in 1889 (p. 20). The formulation of this theory may be taken to mark a distinct advance in the investigation of the subject, and various modifications and applications have been made of its corollaries by several workers. It is notable that Frank (p. 24) attributed the behavior of the plant in darkness to an adaptive reaction on the part of the plant, and asserted that light and darkness exert a direct stimulative effect upon plants, the various organs of which react in a characteristic manner, and that he was not aware that such an explanation had been previously offered (Lehrbuch der Botanik, p. 396. 1892). Thus he says: "Fasst man die hier hervorgehobenen Charaktere der etiolirten Pflanzentheile richtig auf, so gelangt man zu einer ganz anderen Erklärung des Etiolements als wie sie bisher versucht worden ist." And in his discussion of his own interpretation of the matter the following statement is made: "Für alle Organe aber wo Ueberlängerung im Dunkeln sich einstellt, ist diese aber auch wieder in einen anderen Sinne eine vortheilhafte Anpassung, denn sie ist hier ein für gewohnliche unfehlbares Hülfsmittel, um den wachsenden lichtbedürftigen Pflanzentheil schliesslich doch ans Licht zu bringen." Meanwhile Godlewsky's extensive discussion of the subject had previously appeared and his conclusions seemed to be confirmed by the observations of the author and those of F. Darwin in 1896, and Pfeffer[197] has adopted this explanation of the matter in his recent text-book.

Thus he says: "In richtiger Erwägung der Sachlage kann es nicht zweifelhaft sein, dass sich bei dem Etiolement in erster Linie um eine Reizwirkung des Lichtes aber nicht um einen durch Nahrungsmangel verursachten Erfolg handelt." It is to be noted that Palladine saw in the altered forms of etiolated plants the lack of the influence of light in the promotion of transpiration, and the development of the surfaces which ordinarily enlarge the capacity of the plant for throwing off watery vapor, an explanation that has been found to be insufficient to account for the phenomena in question (1890–1893). There remains to be mentioned the proposal of Noll to use the term "etiolation" to designate adaptational elongations which take place for the purpose of carrying foliar or reproductive organs up into their proper media and to exposures of optimum intensity, and to recognize among other forms of etiolation "water-etiolation" by which the stems of aquatics are elongated to bring the leaves and flowers to the surface, "darkness-etiolations" to include the phenomena forming the subject of the investigations to which this memoir is chiefly devoted, and "reproductive-etiolation" to denote the sudden elongation that ensues in propagative and reproductive branches (1902). "Green-etiolates" had already been suggested by Bonnier in this connection to designate the excessively elongated shoots of plants grown in continuous electrical illumination (1895).

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[197] Pfeffer. Pflanzenphysiologie, 2: 114. 1901.

MORPHOGENIC INFLUENCE OF LIGHT AND DARKNESS.

An examination of the groups of facts obtained by absolute etiolations shows most clearly that no one of the theories recorded in the preceding section is capable of general application to the behavior of all plants in darkness. The unusual ductility of the bodies of plants in darkness is a consequence, or accompaniment of the abnormal forms produced by etiolation, not a cause of them, and the extended existence of shoots in darkness and their subsequent behavior when exposed to illumination is signal proof that a shoot absolutely etiolated is not in a pathological condition in the ordinary acceptance of the term, although when a mature green leafy shoot is confined to darkness the leaves and other chlorophyl-bearing members may become more or less pathological, in a manner which might be expected when any active tissue is forced into prolonged inactivity. The " self-nutrition theory" has been abandoned for equally obvious reasons, among which the most important are that leaves (to which this theory principally applies) may be induced to make nearly the full amount of growth, but not of morphological differentiation when stimulated by the removal of concurrent organs. All attempts to establish a direct connection between the action of light on tissues, and the behavior of these tissues in consequence, have so far failed, and the former conclusions as to exaggeration or multiplication of epidermal and other elements are found to be wholly worthless. Furthermore the extension of this idea by which laws of etiolation were formulated as to the behavior of leaves and stems in darkness is found to be entirely unsupported since no classification of the etiolative reactions may be made on an organographic basis. As may be seen from the sections in which this matter has been discussed in the present paper the phenomena exhibited by both leaves and stems are extremely diversified and widely divergent. Lastly, as to the proposal that etiolative reactions are adaptive in their nature it is to be said that the forms presented by the shoots of a greater majority of the species examined do not exhibit any beneficial adjustments by which the plant might free itself from encompassing darkness, and lift its leaves and reproductive organs past the obstruction that intercepts the rays. It needs but a glance at such etiolated shoots and leaves as those of *Aster*, *Bowiea*, *Pastinaca*, *Peltandra*, *Phytolacca*, *Populus*, *Sarracenia*, as well as those of the floating aquatics to demonstrate that the abnormal forms assumed by these plants could not be interpretated, even by the most generous allowance, as being adapted to reaching out to light, or even of maintaining an economical existence during its absence. On the contrary many species exhibit phenomena the reverse of useful, such for instance as the increased diameter of the stems and the positions of the various organs. That some species are capable of adaptations by which shoots or leaves deprived of light make excessive and rapid elongations which have the effect of carrying the apical portion up more rapidly and to greater distances than the normal is to be admitted. Such capacity is to be seen in such forms as *Arisaema* in which the perennial portion of the plant lies deeply buried, and the growth of the aërial members continues until the exposure to light acts as a stimulus which checks further effort in this line. It is to be clearly understood however, that such action is not purely etiolative in its character, but is in fact an adaptation of which the plant is capable when etiolated, and that not all plants have acquired this habit or power of adaptation to darkness, although all green plants undergo etiolative alterations in addition to those accompanying the non-formation of chlorophyl. Etiolation is therefore not an adaptation to darkness, and the forms assumed by plants in darkness are not necessarily, or primarily, due to an effort on the part of the plant to attain exposure to light. The various phenomena of etiolation are due to the absence of light in the first instance, and the forms assumed by plants in this condition may, in some cases, be modified in such manner as to be of benefit to the plant by enabling it to make an effort to thrust its leaves or shoots up into light. This statement applies to the fungi also, some of which have been found to show etiolative adaptations of this character.

Relation of Light and Darkness to Growth, and to Differentiation and Development.— Doubtless the most important and basic fact common to all species, not including degenerate chlorophylless forms, is that the tissues of etiolated organs do not show the same degree of morphological differentiation as may be found in corresponding members of the same age exposed to illumination. The tissues of stems, leaves and floral organs undergo only limited departures from the embryonic, or bud-condition, when grown in darkness, and the varying amounts of differentiation in the separate instances may be infallibly traced to the action of light upon the plant during the period of definitive formation of the organs in question. Thus for example the exposure of the plumule to illumination in a bursting seed, or of a bulb or tuber to the action of light during the previous vegetative season, will be manifest in results in the way of differentiations of tissue carried to a stage beyond that shown by organs laid down and wholly developed in darkness. This non-differentiation is accompanied by more or less growth or increase in volume, and perhaps in number, of the primitive tissue-layers, which may or may not carry the various tracts far beyond their normal size, but which may in consequence give the organ of which they are a part an abnormally large or small size, length, thickness, cross-section or expansion. As a matter of fact a comparison of the normal and etiolated behavior of a plant offers a splendid demonstration of the fact that growth, and development or differentiation, are not only independent but easily separable processes if the action of the factors inducing differentiation is removed or prevented. The lack of differentiation and the augmentation of the rate and amount of growth is most noticeable in the simple tissue-tracts in the medullary regions, and in the cortex, and furthermore these differences are most highly accentuated in branches and petioles. The distinctive characters of the subdivisions ordinarily present in the above regions including the perimedullary layer, the medullary rays, the inner cortex, the median cortex, and the outer cortex (often collenchymatous in its character in normal plants), are almost entirely lost, and appear only in etiolated plants that endure extended periods of confinement in the dark, and then in only a slight degree of the normal differentiation. Endodermis and pericycle were entirely lacking from all perfectly and absolutely etiolated aërial members. From an organographic point of view the least reduction was to be found in the, presumably, most primitive organs and parts of organs, such for example as the hypopodia of leaves, and so far as our information goes a parallel reduction is to be found in the separate tissues. The primary xylem elements appeared in much the usual manner, but the structural development of these elements which is dependent upon changes in the walls including the deposition of quantities of aplastic matter failed in carrying them toward a normal stature and form. The development of the secondary fibrovascular elements is of course dependent on embryonic layers or generative tissues, and as these were not formed in all species the stele often showed great variation from the normal. The incomplete deposition of aplastic material in the membranes affects the mechanical qualities of the organs most seriously, and allows them to remain a much longer period in an extensible condition, and capable of abnormally great growth-extension, although as may be seen, this excessive growth does not always follow. The diminished deposition of aplastic matter in the cell-walls affects the epidermal layers even more seriously than the components of the stele, and as an accompaniment of this increased extensibility and prolonged capacity for division the epidermis exhibits a great variability of behavior in the different species. It is to be borne in mind however, that the failure to deposit material in the membranes may not be attributed to any lack of formative matter, since this is often present in comparatively enormous quantities in completely etiolated plants.

It is to be seen therefore that the phenomena of etiolation rest upon, and consist in the behavior of the plant consequent upon the absence of the morphogenetic influence of light. Some species show an adaptation to this absence of light, or to the positive influence of darkness, by which the shoots or petioles are elongated in such manner as to constitute an effort to escape from darkness, or to attain illumination.

The Stimulative Influence of Light. — It has been so thoroughly demonstrated by the researches of the last half century that the dorsiventrality of many of the lower forms, and the development of branches and other members is dependent upon illumination that no further discussion of the subject is necessary in this paper. Similarly temperatures may affect some of the morphological developmental processes. Every species appears to be attuned to a certain range of intensity of the various environmental factors, and to be capable of carrying out its chief morphologic and physiologic activities only within this range. Failure to obtain the customary exposures means a loss of the stimulating effect of the agent in question, and the activities ordinarily set up by the stimulating action of the missing force do not appear. Thus a low intensity of radiant energy in the form of heat may suffice to cause the plant to grow for a season or even for a term of years, but the stimulating effect of a higher intensity not being furnished, the plant does not develop floral organs, an inhibition of this character following the exclusion of light from a plant. Not only does the formation of certain important members of the shoot fail to occur, but the reduction extends even to the protoplasts, in which multiplication may go on unhindered even beyond the ordinary point, but which do not undergo all of the transformations and differentiations characteristic of the mature plant. The lack of differentiation of the tissues of the more purely mechanical functions would of course be most apparent in the effects produced on expanded lamellar structures, such as leaves, especially in those forms in which the mechanical elements are grouped in complicated anastomosing strands. On the other hand, it is to be readily seen that in leaves with a parallel venation and basal growth, such as those of *Narcissus*, the extension of the leaf does not depend to such a great extent upon the completeness of the differentiation of the tissues, but rather upon the continued formation of additional cells. As a matter of fact such leaves may attain a size, both in width and length, far beyond the normal although the tissues are by no means in a normal condition of maturity.

The same causes would be operative in the development of floral organs and the formation of seeds. No plant has been found capable of carrying the stamens and pistils to functional maturity in darkness. Reduction or atrophy appears earliest in pollen, and the very marked lack of differentiation in the tissues makes impossible the integration of such a mechanically complex body as a seed in absolute etiolations. Some diversity is to be found in the behavior of floral envelopes however, which rest upon causes similar to those which inhibit the development of complex forms and permit the formation of forms of simple structure. Thus the simple spathes of the aroids may reach a much more advanced stage of development than the floral envelopes of *Narcissus* and of other plants which have two circles of organs in the perianth.

The stimulating action of light upon an organism in producing morphological differentiations is not due to any direct action which the rays might exert upon any particular tissue, or to the action of light upon any part of the organ concerned.

The stimulative effect of illumination, like that of many other forces, may be received by one portion of the body and transmitted to another, and the impulses may even be communicated to organs not actually formed at the time the stimulating rays were received.

This is illustrated by the seedlings of *AEsculus* in which a brief illumination of the basal internode, which is the only one developed in normal plants during the first season, set up a stimulus which was communicated to other internodes formed weeks later and in consequence of which laminar bodies arose, which were invariably lacking from absolutely etiolated seedlings (see p. 191). Another phase of this reaction is to be seen in "partial etiolations" in which the terminal portion of a shoot is confined in a miniature dark chamber and the basal portion is illumined in a normal manner. Few experiments of this kind are faultless in providing absolute exclusion of light from the confined organs, and normal conditions of atmospheric humidity, although in some instances care has been taken to secure proper temperatures. The most striking of such tests were made by Jost, in which he found that etiolated leaves might attain dimensions approximating the normal when a portion of the shoot was exposed to light, and also that when only a few of the buds of the beech were exposed to the light, others in darkness, which remained quiescent when the plant was wholly darkened, awoke as a result of the stimulation transmitted to them. The effects of transmitted effects of stimulation by light have been analyzed by Teodoresco, who compared the structure of normal leaves and stems with similar organs formed on plants subjected to "partial etiolation," and also by placing an active green plant in darkness after it had made a certain amount of growth. The organs enclosed in darkness attached to shoots a portion of which was exposed to illumination attained a greater size and a more complete stage of differentiation than those found on plants which were first allowed to make a certain amount of growth under normal conditions and then completely enclosed in a dark chamber. The results here speak most clearly of a stimulative action. The long-continued stimulation received by the exposed portions of the shoot in partial etiolations would naturally be transmitted and produce more marked effects in the way of perfection of tissues and development of size than when the entire plant was placed in the dark room and only the after-effects of previous exposure would be present. Partial etiolations of flowers by Beulaygue resulted in similar differentiations of the tissues of these structures.

The separate and distinct effects produced by the various regions of the spectrum are not easily analyzed. Sachs claimed to have proved that the ultra-violet rays were necessary for the formation of flowers, but C. DeCandolle's experiments showed that, although the production of flowers was reduced in light from which the rays in question had been screened, yet some were formed, so that the action of ultra-violet was not indispensable to the growth and development of these organs. It is not impossible that the results of both observers were due to the diminished intensity of all of the rays consequent upon the experimental methods used. This seems the more probable since the sporangia of *Pilobolus* and other fungi are capable of normal development in the absence of the ultra-violet rays. In a lengthy examination of the influence of the principal divisions of the spectrum Teodoresco found that the development and differentiation of the tissues of the leaves and stems was most nearly like that of etiolated plants in green light, more nearly perfected in red and that these organs were most highly developed in blue-violet rays. These results however, are not capable of any simple interpretation since the phenomena obtained by exposure of a shoot to any restricted portion of the spectrum must be complicated by the intervention of the specific absorption of the rays by chlorophyl, and also by the heat of the rays used. It is, of course, not improbable that the more refrangible rays may exert a stronger morphogenetic stimulation in the same manner that they have the greatest phototropic influence of any portion of the spectrum. Outside of these considerations it is to be noted that the development and differentiation of any tissue is more or less dependent upon the functional activities devolving upon it. The removal of any condition incident to the proper performance of a function, inhibiting the function itself may result in the atrophy, partial or complete, of the organs concerned. Leaves are examples which illustrate this regulatory device most clearly. The capacity of the plant for cutting off mature foliar organs which have been rendered functionless by any cause is well known and has long been recognized. Both phases of this relation are exhibited in the tests which have been made with the growth of shoots in atmospheres lacking carbon dioxide. In such experiments in which plants are used that are furnished with reserve food, the leaves and stems make a rapid growth with lessened differentiation owing to the inhibition of the photosynthetic function, while mature leaves already formed are cast off as a result of their uselessness. The amount of action shown by young leaves cultivated in atmospheres lacking carbon dioxide has been expressed in one of my contributions to this subject as follows: "The greatest divergences of reaction appear during the second or unfolding stage. The leaves of some plants quickly perish at the beginning of this stage if in an atmosphere free from carbon dioxide; others carry on a more or less complete development before perishing; others attain a size somewhat less than the normal, and then continue to live in an apparently healthy manner; and others attain a normal size, and continue existence showing no deviation from the normal." It was also demonstrated that the casting away of useless or functionless organs was also a matter of morphological constitution to some extent and that some species are not capable of this adaptive reaction.[198] A similar state of affairs is to be predicated of organs grown under etiolative conditions, and the form of the plant when cultivated in darkness must be a result of the lack of the specific morphogenetic influence of light and also of the lack of functional activity of such organs; although it is not to be taken for granted that all leaves on all plants are functionless in darkness. On the contrary the organization of the shoot is such, in some instances, that the entire amount of transpiration is carried on by the etiolated leaves, and the needs of respiration may also operate to stimulate the development of the tissues to some extent. The varying importance of what may be termed these minor functions may be taken to account for the different degrees of development and differentiation reached by various etiolative organs in darkness; and it is to these factors that at least a portion of the increased development of the leaves and shoots when freed from the competition and aid of concurrent organs in darkness must be ascribed.

Some highly interesting considerations are raised by the results of Bonnier in the culture of shrubs in continuous electrical illumination and by the experiments of Browne and Escombe (p. 274), in regard to the size and development of leaves and internodes. The development of leaves in atmospheres containing abnormally large proportions of carbon dioxide, in which an increased photosynthesis occurred, resulted in these organs attaining sizes below the average, and also resulted in the formation of stems of about the usual length but composed of a greater number of internodes than the normal, which were, of course, shorter than the normal average. On the other hand, the development of shrubs in continuous illumination of an intensity which reduced photosynthesis to one-third the average rate in sunlight also resulted in the development of leaves which did not reach the average normal size, while the branches on which they were borne were more slender, attenuated and with internodes longer than the normal. In both instances the amount of chlorophyl present seemed to be greater than usual. The more prominent features of the development of plants grown under such weak constant illumination are more nearly like those of specimens grown under discontinuous diffuse light, both as to the size of the leaf and the development of the stem. Whatever differences are to be seen may be attributed to the fact that in the case of the plants grown under constant illumination the stimulating action of light was never absent, and to the fact that the total amount of material resulting from the photosynthetic processes must have been much greater than in plants which were exposed only a portion of the day to diffuse light. It is to be said that certain features of Bonnier's results need further investigation before any generalizations might be safely made concerning them. Thus for instance, it is not clear why plants grown in discontinuous electrical illumination should more nearly resemble normally grown plants than etiolated ones, which those grown in continuous illumination resemble, a result that is confirmed by Bailey, Rane and Corbett. Several important conclusions might be drawn from a superficial inspection of the results in question. The exaggerated length of plants grown under conditions

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[198] MacDougal. Relation of the growth of leaves and the chlorophyl function. Jour. Linn. Soc. London, 31: 525–546. 1896.

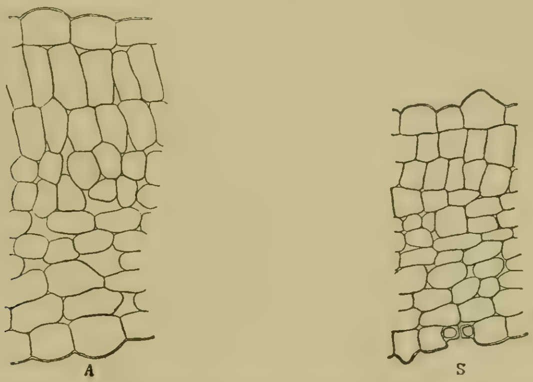

FIG. 172. *Lupinus albus*. *A*, partial transverse section of normal leaflet. *S*, partial transverse section of leaflet grown in an atmosphere lacking carbon dioxide. After Teodoresco.

in which the proportion of time during the vegetative season in which exposure to light takes place, would apparently indicate that the action of light actually accelerates growth, at least when under a certain degree of intensity, and that the amount of growth made by a plant would be correspondent to the actual length of time of illumination which it undergoes. The increased photosynthetic activity of the plant under constant illumination would offer some features different from those of specimens grown in atmospheres enriched in carbon dioxide. In the latter instance a greatly accelerated production of carbohydrates takes place during the day, and at a rate wholly beyond the capacity of the translocating and assimilatory apparatus, in consequence of which the leaves are not carried to their maximum size on the one hand, and such plants actually become pathological after a time. The increased photosynthetic activity of the plant with a lengthened day is not due to an increased rate, but to a continuation of the process at a diminished rate during the entire twenty-four hours — at a rate that allows the entire product to be handled in the usual manner by the assimilating and conducting mechanisms.

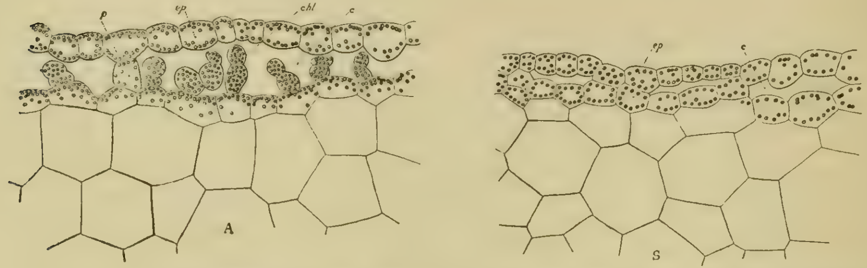

FIG. 173. *Marchantia polymorpha.* *A*, transverse section of thallus cultivated in an atmosphere containing carbon dioxide. *S*, section of thallus grown in an atmosphere lacking carbon dioxide. After Teodoresco.

As to the difference in results between continuous and discontinuous illumination, the only solution of the problem that presents itself is the supposition that, the alternating action of light and darkness, rather than continuous light, constitutes the stimulus that sets up the morphogenetic action ascribed to the action of illumination.

The stature or relative mechanical positions assumed by the various members of the shoot under etiolative conditions presents a phase of the subject not directly tested in many of the experimental observations. It is noteworthy however, that nearly all stems examined exhibited negative geotropic reactions, and assumed an upright attitude at least as to the terminal section. Thus many etiolated stems fell over because of their lack of mechanical rigidity when the apical portions again began to ascend in consequence of the upward curvatures of the tip. This was also true of a large number of bilateral and dorsiventral leaves arising from underground stems and rhizomes. Branches were shown in a manner offering evidence of value only in *Asparagus* and *Populus* and in both of these instances the position seemed to be due directly to apogeotropism, and the angle made with the axial member was often much smaller than in the normal shoot. Leaves arising from aërial shoots in most instances were more nearly upright than in illuminated specimens; in some instances this altered position by which the angle of the petiole with the stem was diminished, might be ascribed to apogeotropism, while in the greater majority the position seemed to be due simply to the autotropism of the plant, and the position of the petioles was a matter of the growth of the tissues of the petiole, controlled entirely by the regulatory mechanism of the organism. Coincidently with the assumption of such positions on the part of the axes of the leaves the laminae were generally held in a plane continuous with that of the petiole or but little divergent from it. A number of species including *Acer*, *Cornus* and others were examples of a class in which the much reduced leaves were supported in a position quite similar to that of the normal. *Polystichum acrostichoides* is an example of a leaf in which the position of the terminal portion of the leaf is clearly due to the action of light.

ILLUMINATION OF ETIOLATED PLANTS.

The phenomena consequent upon the exposure of an etiolated shoot to light consisting of alterations in position, awakening activity of dormant organs, and alterations in the methods and rate of growth and development seem capable of interpretation only in the light of the conclusions reached above as to the nature of etiolation. An etiolated shoot is one in which the length of the main axis, and of the axis of the foliar organs is often much greater than in the normal organs, and the various organs are held in positions much different from those customary in the several species, while the bulk of the stems and leaves is composed of a mass of cells very imperfectly, or scarcely at all differentiated toward their final form, and but little adapted to the performance of the normal functions, being in a much more embryonic condition. Whatever development may be incited in such plants takes place under extraordinary conditions. The amount of tissue present in which differentiation might ensue is much greater than the ordinary because growth has taken place without morphologic changes ensuing in an equal manner. Again, the leaves and other organs are in a position divergent from the normal, and their assumption of the normal attitude is to be made by a mechanism consisting of tissues not made up in the same manner as the normal.

Illustration of the action of a monocotyledonous species with netted venation of the leaves is afforded by the observations on *Arisaema triphyllum* (Fig. 14, and also p. 60). Here the etiolated petioles and scapes have reached a length beyond the normal before being illuminated, and this stature appears in the final position of the plant after illumination. Futhermore, the form and position of the folioles are different from the normal and they do not reach the full expansion. The most marked deviations from the normal are offered by the spathes. These organs are more slender than the normal when etiolated and the normally over-arching hood is held in a position approximately upright, that is in continuation of the plane of the lower portion of the spathe. Exposure of such etiolated spathes to light resulted in every instance in such excessive growth of the tissues of the inner surface that the hoods were curved outwardly until a position nearly horizontal was reached with the inner surface uppermost.

The illumination of etiolated specimens of *Asplenium platyneuron* (p. 78 and Fig. 31) resulted in the development of the pinnae, and in the assumption of a recumbent position of the leaves. Etiolated leaves of *Peltandra Virginica* (p. 147, Fig. 102) showed some further elongation of the petioles after exposure to diffuse daylight, but the most striking feature consisted in the reactions of the laminae, which moved from the upright etiolated position to one approximately horizontal. During this process the laminae which were below the normal size expanded so irregularly that one of the basal lobes reached a size two or three times as long as the other giving the leaf a very unsymmetrical appearance. *Polystichum acrostichoides* developed etiolated upright leaves with the pinnae retained in tightly rolled clumps, and when these organs were illuminated the pinnae made a development which did not carry them far enough to constitute normal structure, while the rachis made a pronounced curvature below the lowermost pinnae in such manner that the upper portion of the leaf was held in a position fairly horizontal.

The positions assumed by such etiolated organs after illumination have been held by Detmer to be due to *photo-epinasty* and *photo-hyponasty* (see p. 14), or to special relations of the rate of growth of the opposite flanks of dorsiventral organs induced by illumination.

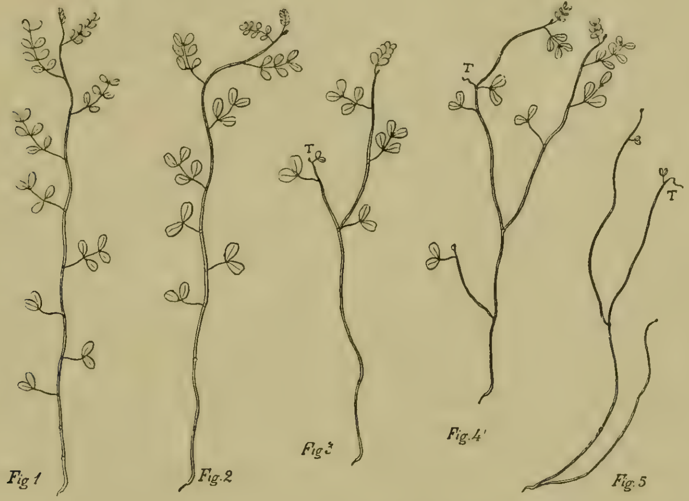

FIG. 174. *Ervum Lens.* 1, specimen cultivated in normal illumination; 2, plant cultivated in darkness five days, then illuminated; 3, plant cultivated in darkness eight days, then illuminated; 4, plant cultivated in darkness thirteen days, then illuminated; 5, etiolated plant. After Ricome.

So far as leaves are concerned the movements in question are such as to carry the laminae to a normal position, but in the case of the foliar hood of the spathe of *Arisaema* it has been seen to place this structure in an extraordinary recurved position in which it must be wholly useless as a floral organ. While it seems entirely clear that the comparative rates of growth of the two halves of a dorsiventral organ may be radically modified by illumination, yet the action in question is a general one, and does not necessarily entail any special relation of light to this phase of the activity of the plant. On the contrary the growth of the tissues in darkness occurs, as has been pointed out, as a matter of simple increase of the volume of the tissues without the customary differentiation of the elements, and it is to this unguided action that the epinasty or hyponasty of an etiolated organ is due, which may be different from that of a normal green member.

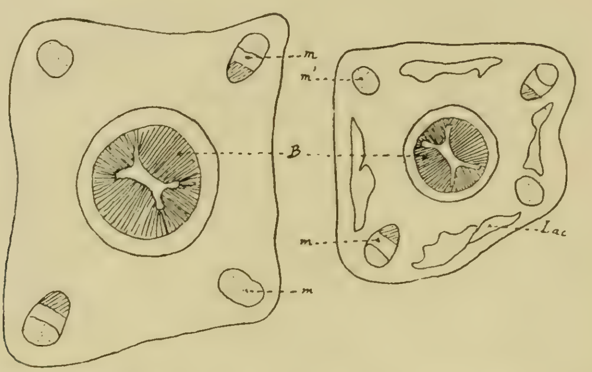

FIG. 175. *Ervum Lens.* *A*, transverse section of normal stem; *B*, transverse section of etiolated stem which has been illuminated, showing cortical lacunae. After Ricome.

In other words the various phases of reaction shown by plants in darkness are not to be ascribed to any direct lack of the stimulating action of light, but rather to the fact that when this stimulating and determinative influence is lacking a most complex and closely correlated series of happenings follow, all of which are more or less closely concerned with the primary reaction of growth and increase of volume of various tracts of tissue unaccompanied by the ordinary differentiations and transformations of tissue; transformations, which entail not only the conversion of great quantities of plastic into aplastic matter, the death of large numbers of cells, but also most serious changes in the mechanical qualities of the membranes and the protoplastic enclosures.

The most serious investigation of the behavior of etiolated plants when illuminated has been carried out by Ricome, but unfortunately his observations seem to have been confined to seedlings. The plants examined were grouped in three classes according to the action of the cotyledons in germination, and the amount of reserve material present. The greater length attained by some species in darkness was maintained for a time after being exposed to light, but eventually the plants which had been normally illuminated reached the greatest length of stem. The internodes which developed on etiolated stems immediately after exposure to light were something shorter than homologous members of normally illuminated shoots. During the process of transferring etiolated plants from darkness to light many leaves and often portions of the shoot were killed by reason of the desiccation consequent upon the accelerated transpiration. The retarded growth of the younger portions upon illumination was ascribed to this exaggerated loss of water. Upon the illumination of etiolated seedlings the new processes including differentiation of the tissues and of a generative layer set up such tensions in the cortex and epidermis that these tissues were not able to keep pace with the extensions and were ruptured and crushed. Ricome did not regard etiolated organs as pathological, because of the fact that after illumination they were capable of carrying out a development fairly approximate to that of the normal if a proper supply of constructive material were provided. Thus, in the case of *Ricinus*, leaves formed under etiolative conditions were seen to attain a size in excess of the normal in some instances when illuminated. In no instance does this author find any warrant for an assumption that the action of light retards growth, although the length attained by internodes and organs might be less by reason of the actual desiccation consequent upon increased transpiration caused by light.

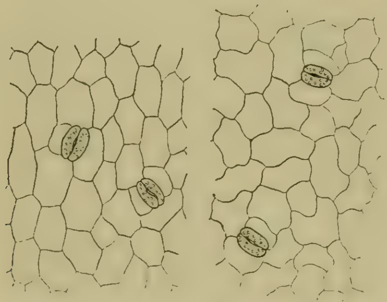

FIG. 176. *Ricinus communis*. *A*, normal epidermis from ventral (upper) surface of leaf; *B*, epidermis from ventral surface of etiolated leaf. After Ricome.

INFLUENCE OF ETIOLATION UPON CHEMICAL COMPOSITION.

A very noticeable effect of etiolation consists in the retarded development of glandular organs and a diminution of the formation of substances to which odors are due.

DeCandolle[199] was perhaps the first to record that "savours" and "odours" were not so highly developed in etiolated plants, and similar facts were obtained by myself notably with *Amorphophallus*, in which the offensive odor is but little marked in individuals grown in darkness. On the other hand, Schübeler[200] found that north temperate species taken northward and allowed to grow during the two months' day in Scandinavia developed a noticeably larger amount of aromatic and flavoring substances. This feature is also to be seen in celery which has been properly blanched, the characteristic flavor lacking some of the rankness found in fresh green stems. Etiolation then may be looked to as a method of reducing the strong and rank flavors of many plants in the effort to make them of economic use, and Morren[201] estimated in 1863 that about two hundred species of known plants might be capable of improvement as an article of food by the etiolating treatment. It is to be seen however that the etiolation of a plant does not actually increase the amount of material of nutritive value to the human body. The chief merits of the process consisting of the reduction of the ranker flavors and the diminution of the amount of cellulose present, rendering the material more attractive as food, and more easily masticated.

The constant respiration carried on by etiolated plants must of course result in the combustion of a large amount of plastic material, while on the other hand not so much of the plastic substance is converted into aplastic form in the manufacture of cell-walls in permanent tissues. According to the researches of Palladin[202] etiolated stems contain much less proteinaceous material than the normal.

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[199] DeCandolle, A. P. Physiologie végétale, **3**: 1075. 1832.

[200] Schübeler. The effects of uninterrupted sunlight on plants. Nature, **21**: 311. 1880.

[201] Morren, E. La lumière et la vegetation. La Belgique Horticole, **13**: 165. 1863.

[202] Palladin, W. Eiweissgehalt der grünen und etiolirten Blätter. Ber. d. deut. Bot. Ges. **9**: 194. 1891.

Etiolated leaves of "stemless" plants also were much poorer in proteids than green organs of the same species, while etiolated leaves borne on aërial stems were richer in protein than normal green leaves. These results were obtained from examinations of etiolated and normal specimens of beans and wheat.

The data obtained in my own analyses may be restated in the form of the following tables:

WATER, DRY MATERIAL AND ASH IN CORMS OF *Arisaema*.

	Normal.		First Etiolation.		Second Etiolation.	
Water	89.84	per cent.	82.50	per cent.	80.14	per cent.
Dry material	19.16	"	17.50	"	19.86	"
Ash in fresh material	.306	"	.286	"	.453	"
Ash in dried material	2.44	"	1.63	"	5.89	"

WATER, ASH, AND DRIED MATERIAL IN LEAVES OF *Arisaema*.

	Normal.		First Etiolation.		Second Etiolation.	
Water	91.105	per cent.	93	per cent.	96.24	per cent.
Dried material	8.895	"	7	"	3.76	"
Ash in fresh material	.404	"	.519	"	.366	"
Ash in dried material	4.54	"	7.43	"	9.73	"

It is thus to be seen that the proportion of water in corms formed during etiolation is less than under normal conditions, and this decrease continues in the second etiolation, in which the percentage is higher than that of resting corms dried in the air at ordinary temperatures (p. 61). At the same time the proportion of dry material increases, although the actual amount is less of course. The proportion of ash in corms formed as a result of the first etiolation is less than the normal, and undergoes an increase in the second season's growth in darkness. In like manner the proportion of ash in the dried material is less than the normal in corms resulting from the first etiolation, but increases during the second etiolation to a percentage much greater than the normal in fresh corms and greater even than in air-dried corms. These results point quite conclusively to an accumulation of ash in the body of the plant during its successive seasons of development when confined in the dark room.

The proportion of water in the leaves is greater than the normal during the first etiolation and shows a further increase during the second growth in darkness. The dried material undergoes an inverse alteration. The proportion of ash in the fresh material increases during the first etiolation and decreases in the second to a point below the normal. When a comparison is made with the dried material, however, the proportion of ash is seen to increase during the first as well as in the second etiolation, in which it about doubles the normal proportion. The small proportion apparent in fresh material of the second etiolation is due to the great increase in the percentage of water present. The increase in the proportion of ash to the dried material during the first and second etiolations is seen to be due to the lessened formation of dried material rather than to any positive increase in the amount of mineral matter carried up into the leaves as an accompaniment or result of etiolation.

André found that an increase of temperature of the higher plants between 15 and 30° C. increased the amount of silica carried up in etiolated shoots. The amount of calcium carbonate was decreased and the quantity of potassium and phosphoric acid remained about the same. The proportion of vasculose among the hydrocarbons was increased. It is difficult to account for the increase in the amount of such an insoluble substance as a result of higher temperature and increased transpiration.[203]

Interesting comparisons are afforded by the data obtained by Karsten[204] with seedlings of *Phaseolus multiflorus*, which were allowed to grow 15–20 days in the light and others 25 to 30 days in darkness. By reason of the longer period of development in darkness the total weight of the etiolated plants was much greater than it would be if taken at the same age as the normal examples. The relative composition of the separate organs is shown in the following tables:

PROPORTION OF DRIED MATERIAL IN SEEDLINGS OF *Phaseolus multiflorus* AFTER KARSTEN.

	Leaves.	Hypocotyl.	1st Internode.	2d and 3d Internodes.	Roots.	Cotyledon.	Average.
Normal	15,878	16,646	13,090	12,100	8,379	21,554	15,502
Etiolated	16,959	6,668	8,731	8,194	7,509	17,574	11,431

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[203] See André, G. Action de la temperature sur l'absorption minerale chez les plantes etiolées. Compt. Rend. 134: 668–671. 1902.

[204] Karsten, H. Die Einwirkung des Lichts auf des Wachstum der Pflanzen. Jena. 1870.

The following table by Karsten shows the actual amount of fresh and dry material in a lot of plantlets produced by seeds weighing 1,000 grams, under normal conditions and in darkness :

NORMAL.

	Leaves.	Hypocotyl.	1st Internode.	2d and 3d Internodes.	Roots.	Cotyledon.	Total.
Fresh	722	115	393	222	1,038	1,551	4,041
Dried	114	12.3	51.5	26.8	87	334	626.5

ETIOLATED.

	Leaves.	Hypocotyl.	1st Internode.	2d and 3d Internodes.	Roots.	Cotyledon.	Total.
Fresh	134	293	1,437	570	832	1,582	4,886
Dried	22.6	19.6	127.3	46.7	62.4	277.7	556.2

The superior weight of dry material in the internodes and hypocotyl is the result of the greater age of the etiolated specimens, while it is to be seen that the construction of dry matter in the roots has fallen below that of plants with green stems and leaves (see p. 25).

The following table by Karsten gives the number of parts of the principal constituents of the dried material (at 105° C.) in 100 parts of normal and etiolated plantlets and in seeds. The figures are given to the nearest decimal of the first place and the data obtained from normal plants is given in the column under A, and from etiolated plants under B.

	Leaves.		Hypocotyl.		1st Internode.		2d and 3d Internode.		Roots.		Cotyledons.		Seeds.
	A	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*	*B*	*A*
Fats	4.9	4.15	3.5	3.48	2.69	2.54	3.9	3.16	2.55	3.13	2.7	2.79	1.18
Sugar	.11			.39	.585	.166	.438	.02	.39		3.86	2.93	8.84
Gums	20.21	18.	19.2	18.1	14.9	14.6	18.89	15.53	14.5	14.	16.4	13.1	12.9
Starch	1.3	1.7	2.8	2.4	3.	3.5	2.5	2.2	4.7	4.8	19.9	19.	18.4
Cellulose	9.7	9.1	21.3	15.9	22.7	20.3	20.	24.	18.9	19.3	3.9	4.	4.
Protein	36.3	53.3	24.4	35.7	27.5	43.1	29.4	38.1	24.41	33.8	21.9	20.2	21.9
Ash	5.9	10.9		11.1	4.2	6.3	8.2	9.5	5.3	6.	5.7	5.3	4.2
Residue	21.7	2.9	28.8	12.9	24.4	9.3	16.9	7.4	29.3	19.	26.4	32.7	36.
Nitrogen	5.8	8.5	3.9	5.7	4.4	6.9	4.7	6.1	3.9	5.4	3.5	3.2	35.

The proportion of fats is seen to decrease in the leaves during etiolation, to remain stationary in the hypocotyl, to decrease in the stem, and increase in the roots.

The proportion of sugar undergoes a marked decrease during etiolation throughout the entire plant, the greatest percentage remaining in the cotyledons. The amount of starch was greatest in etiolated leaves, normal hypocotyls, etiolated first internodes, normal internodes above etiolated roots, and normal cotyledons. Cellulose was present in smaller proportions in etiolated leaves, hypocotyls and lower internodes, and in greater proportions in etiolated upper internodes, roots and cotyledons. These determinations of cellulose are undoubtedly faulty, especially in the stems. Protein was present in greater proportion in etiolated leaves, hypocotyls, stems and roots, and in smaller proportion in cotyledons than in the normal. These results do not agree with those obtained later by Palladin (p. 23). The amount of ash in a given weight of material was greatest in etiolated leaves, hypocotyls, internodes and roots, and less in cotyledons than in the normal, which is in general agreement with the results obtained in my own analyses. Rzentkowsky's[204] examination of seedlings of *Phaseolus multiflorus* led him to conclude that etiolated plants do not take up mineral substances from the substratum a conclusion which is undoubtedly wrong, as demonstrated by André and myself.

THE RATE AND MODE OF GROWTH AS AFFECTED BY LIGHT AND DARKNESS.[205]

The rate of growth of any organism varies in such manner that a more or less irregular acceleration is shown during the earlier stages of development until a maximum of increase is reached, when a similar diminution brings the action to zero. Minor maxima are also shown before or after the major in some instances. In addition to this major movement which traces the curve of the grand period of growth of the organism, minor deviations occur, which may be due to alterations in temperature, food-supply, moisture and other causes. Running through the major and minor alterations as above there are seen to be more or less regularly recurring accelerations and diminutions of the rate, which have been shown to be due to a rhythm set up by inherent causes. Baranetzky[206] concluded that the rhythm exhibited by plants in a dark room was an after-effect due to the lasting influence of alternating exposures to daylight and darkness, and pointed out that in continued confinement the diurnal periodicity was lost and the variations no longer occurred with sufficient regularity to constitute a rhythm. Sachs seems to have been the first to formulate the opinion that light retards growth and his position with regard to minor periodicities may be best given in his own words: "I, on the contrary, am of the opinion that in the plant, or at any rate in its growing parts, periodic variations occur in some way quite independent of variations of temperature and light; and these, as I conclude from Baranetsky's observations, may continue for periods of very different lengths. If now the plant is subjected to the regular alternation of day and night, and the variations of temperature are very small, the above-mentioned influences on growth make their appearance, by which its maximum is transferred to the morning hours, and its minimum to the evening, the above-mentioned periodicity arising from purely internal causes being concerned as the weaker factor in a definite daily period of time."

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[204] Rzentkowsky, T. Untersuchung ueber Entwickelung des etiolirten *Phaseolus multiflorus*. Mitth. d. Universität z. Warschau. 1875. Abstract by Batalın in Bot. Jahresber. 4: 745. 1875.

[205] Presented before the Botanical Society of America, at Washington, D. C., Jan. 1, 1903.

Sachs[207] did not agree with Baranetzky however in the assertion that the daily periodicity of plants in darkness was an after-effect of light or temperature, and Vines took the position that the coincidence of the variations with those of normally illuminated plants was probably accidental, although he conceded that the daily periodicity of a plant continued for several days after it had been confined in a dark chamber. Both Sachs and Vines[208] held that it was improbable that the periodicity of fully etiolated plants was due to after-effects; indeed Sachs adduces the fact of periodicity in such a plant as a refutation of the theory of after-effects in the matter, and likens it to the starting of pendulum spontaneously after it had come to rest.

It is to be seen however, that geotropic and other stimulatory effects may be hindered and the response delivered long afterward, and Darwin and Pertz have shown by a beautiful series of experiments that geotropic rhythms may be induced in stems, which are maintained after the stimulus is withdrawn. The position taken by

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[206] Baranetzky, J. Die tägliche Periodicität im Langenwachstum der Stengel. Mem. d. l'Acad. Imp. d. Sc. de St. Petersbourg. Ser. 7. 1879.

[207] Sachs. Physiology of Plants. Eng. Ed., p. 560. 1887.

[208] Vines, S. H. Physiology of Plants. p. 403. 1886.

Baranetzky therefore, that the periodicity of growth maintained by a plant after it has been deprived of illumination, is an after-effect, and which supported by Vines seems well defended, to whatever this daily periodicity may be due. Furthermore, it might be expected an organ would carry on growth with a rhythm due to the action of factors concerned with an extremely early stage of its existence. It is probable that the behavior of any single species however, may not be safely predicted. Thus the auxanometric measurements of *Arisaema triphyllum* disclose a rhythmic action, quite as well marked as that of the normal plant, when grown in a dark room at constant temperatures (pp. 68–70).

The measurements of a leaf of *Quamasia* during a continuous period of fifty days in a dark room at a constant temperature (p. 86) gave opportunity for observations of growth under conditions in which the food-supply, moisture, temperature and darkness were practically uniform. A consideration of the facts shown in the curve plotted from the auxanometric data brings to light the fact that the variations in this instance were exceedingly irregular, and seemingly subject to no rule of any kind. No control observations were made on this species for the purpose of obtaining the variations in normally grown plants. The variations of *Arisaema*, on the other hand, were fairly parallel to those of the specimens under normal alternations of daylight and darkness with the temperature fluctuating.

The observations described in this memoir, together with the records of previous investigations upon etiolation demonstrate most conclusively that the growth of the aërial organs of green seed plants in darkness is not accompanied by the usual degree of differentiation of the several tissues. The amount of growth, or increase in volume, that may be accomplished by the shoot by the extension of the imperfectly developed tissues in the absence of illumination is subject to great variation. In many species the total length, diameter and volume of the etiolated shoot, and its various members is not so great as in the normal, and the rate of growth may not be so rapid as in the normal. The buds and seeds of a number of species, and also the spores of many pteridophytes will not awaken from a resting condition and begin the growth leading to the development of the shoot except under the influence of light. On the other hand, some species of the higher plants, as well as some of the lower forms, carry on the growth of the main axis at an accelerated rate in darkness, and to such an extent that shoots are formed which may exceed the normal both in length and diameter.

It is obvious that, in the above phenomena, the effects are due to the stimulating influence of light, and of darkness (or absence of light). The differentiation of the tissues, and the development of certain reproductive bodies constitute positive reactions to the stimulating influence of the rays, and the exaggerated elongations shown by many shoots is a response to darkness, which may be adaptational in its character, and which might serve to lift the chlorophyl-bearing organs past an imaginary obstruction into illumination. The failure of a large proportion of the forms examined to make an accelerated or exaggerated growth when freed from the influence of light, even when provided with an adequate food supply, shows that light has no invariable and universal relation to increase in length, or thickness, or to the multiplication or increase in volume of the separate cells.

When a green plant is suddenly deprived of illumination a marked acceleration of the rate of elongation ensues, and a diminution ensues when a plant is brought from darkness into light, which Pfeffer, as a result of a consideration of the investigations upon this point, estimates to amount to changes in the rate not greater than fifty per cent. of the existing rate. Many of the observations bearing upon this point were made with plants which do not exhibit an abnormal elongation in darkness. In my own investigations the peduncles and scapes of *Arisaema*, which had ceased to make an amount of growth equal to a total of 1 mm. per day, underwent a comparatively enormous acceleration which reached a maximum about twenty-four hours after being deprived of illumination, and then decreased to a minimum correspondent to the original rate in about a hundred hours. *Arisaema* is a plant which shows a marked adaptational elongation in darkness during etiolation, and this increase may only be ascribed to the stimulative action of darkness, since it would be an obvious absurdity to ascribe such an enormous increase in rate to the absence of any direct or paratonic action of light. This seems still more justifiable when it is pointed out that the rate of growth is never diminished by the action of light to the extent that it is by temperature.

It is clear therefore, that no evidence is afforded by the behavior of plants in darkness to support the conclusion that light directly affects the rate of growth, since not all species exhibit increased growth when freed from its influence, and the accelerated rate shown by mature organs when placed in darkness may be only ascribed to a stimulative action and an adaptational response.

Another aspect of the effect of light on growth remains to be considered. It is well established by hundreds of observations that the rate of growth of a large number of normal greenorgans, or of shoots, decreases when deprived of illumination for a period, such as that of an ordinary night, or even briefer, and then suddenly exposed to the action of the rays. This has given rise to the generalization that light exerts a direct or paratonic action on growth.

Now it has been demonstrated most conclusively that light does not exert any direct effect on the growing region either in the way of influencing cell-division, or the processes depending upon the motility of the protoplasm, or of the material entering into the construction of the membranes. In fact none of the phenomena of etiolation or of diminished growth in light may be ascribed to the direct influence of light upon the tissues or cells concerned but rather upon the organism as a whole. The lessened increase in volume taken into account in measurements of the growth of plants exposed to the action of light may be due to one or both of the following causes. First, it is to be pointed out that the action of the rays on any mass of protoplasm is to accelerate the rate of transpiration, and the loss of water may be sufficient to cause a decrease in bulk, which might neutralize the outward effects of the actual constructive processes, which may continue uninterrupted during the apparent decrease or cessation of growth. On the other hand, it is entirely probable that some of the apparent retardation may not be due to a direct mechanical influence of the rays, but is a stimulative reaction. That the slowing down of the rate of growth under the influence of light is an irritable response is supported by the behavior of plants exposed to continuous illumination for long periods, such as might occur in the polar regions, and which has also been brought about in several series of experiments. In the former instance the specimens grown in localities in which the daylight period embraces the entire vegetative season of several months, the shoot and its members did not exhibit an increase, which either in rate or amount would justify the assertion of a direct retarding influence. The same results have been attained in another form by the exposure of growing plants to continuous exposure to electrical illumination, or to an illumination in which daylight was supplemented by nocturnal illumination from electric arcs, or flames. In all such instances the amount of growth, as indicated by the length of the shoots and of the separate members, was greater than under ordinary conditions of alternating daylight and darkness. If light exerted a direct retarding, or paratonic influence upon the processes of growth, such results would be impossible. On the other hand, if the slowing down of the increase of shoots when suddenly exposed to light is due to a stimulative action the continued illumination of a plant to the action of the rays would soon result in an accommodation to the continuance of the stimulation, and the behavior of the plant after becoming attuned to increased illumination would embrace some features due to the altered conditions of nutrition, and to the supposedly disintegrating effects of the blue-violet rays on chlorophyl and other substances.

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